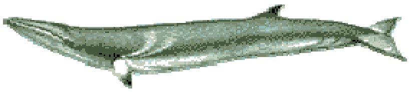

MULTI-SPECIES MODELS OF ANTARCTIC KRILL PREDATORS: DO COMPETITIVE EFFECTS INFLUENCE ESTIMATES OF PRE-EXPLOITATION WHALE ABUNDANCE AND RECOVERY?

by

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Abstract

Many species of baleen whales and seals in the Southern Hemisphere were subject to intensive overexploitation by commercial harvesting in the last two centuries, and many populations were reduced to very low levels. Krill is the dominant prey item of these species. Harvesting (to near extinction) of the large baleen whales (blue, humpback and fin whales) from the start of the 20th century led to a likely increase in the availability of krill to other krill predators such as the Antarctic minke whales and crabeater seals. This phenomenon is referred to as the “krill surplus” hypothesis and has been a central hypothesis of Antarctic ecosystem studies. This thesis aims to better understand species interactions in the Antarctic through developing and extending multispecies models of the system. The study considered only Region A (IWC Management Areas II, III and IV, 60°W to 130°E) because the numbers of baleen whales harvested in Atlantic/Indian Oceans were far greater than in other Oceans, so that the impacts on the dynamics of these species are likely greater.

The simple models of competition between blue and fin whales developed give qualitatively similar results to the Mori-Butterworth Antarctic ecosystem model of an initial number of fin whales before exploitation began that is much lower than single species models suggest. However, there are important features of blue and fin whale CPUE data off Durban over the middle decades of the last century that are not reflected by the model results, and a number of possible reasons for this are advanced. In particular, the introduction of competition in the models predicts a steady fin whale population until 1950, but cannot reproduce the feature in the CPUE data of an increase from the 1920’s to 1950’s.

The study then extends the Mori-Butterworth Antarctic ecosystem model by adding squid, which has fast dynamics compared to whales and seals. The model estimates population trends in terms of numbers or biomass. This study indicates that results are particularly sensitive to the density dependence assumed for natural mortality and/or birth rate. The results highlight that the squid biomass trajectory is relatively insensitive to initial squid abundance but depends strongly on the density dependence assumed for squid.

Generally, the estimated historical trajectories suggest that the inclusion of squid in the model hardly impacts the maxima reached by other species that benefited from the krill surplus. The model predicts that squid started to increase at about the same time (1920) that the reduction of large baleen whales (blue, humpback and fin whales) commenced under heavy harvesting. This suggests that species with fast dynamics such as squid were possibly the first to benefit from krill surplus, even before minke whales and crabeater seals, which started to increase only about a decade later. The study provides a potential framework for understanding the interplay between species with slow and fast dynamics.

1 Introduction

Marine mammals are generally located near or at the top of marine food webs (Pauly *et al*., 1998). The impact that fishing operations may have on marine mammals and other components of marine ecosystems is a major concern today. In the past century the majority of marine mammal populations were reduced to very low levels and, despite extensive management efforts, some species have shown little recovery. On the other hand the recovery of some species may directly or indirectly affect commercial fisheries through reducing the abundance of the species targeted by the fishery. Indirect interactions may occur principally because commercial fisheries and marine mammals frequently target the same species (Plaganyi and Butterworth, 2005).

In this study the impact of commercial fisheries on marine mammals in the Antarctic and *vice versa* is explored. Despite its great natural value, the Antarctic is a heavily transformed ecosystem due to the largest human-induced perturbation of a marine ecosystem in the world (Mori and Butterworth, 2006). Baleen whales and seals are among the most important predators in the Antarctic ecosystem and have been subject to heavy harvests in the past. Since most of this harvesting stopped three to five decades ago, there are now queries as to whether the populations are currently recovering and if so, what the implications are for other species in the system. A number of studies have been undertaken to address this issue in the Antarctic sector in different ways. For instance, some studies focus on the recovery of baleen whales (for example Bannister, 1994; Branch *et al*., 2004; Matsuoka *et al*., 2005) and some focus on which species increase following the depletion of other species (for example Mori and Butterworth, 2006).

The thesis first provides a review of the application of different multispecies models as tools for evaluating the impacts of fishing on marine mammals and vice versa (Chapters 1 and 2). The background to the biology of species included in the models is presented in Chapter 3. The objectives of this study and the methods used are described below. The methods are divided into two parts: Chapters 4 and 5. Chapter 4 describes the model to determine fin whale historic abundance and Chapter 5 describes the extended Mori-Butterworth Antarctic ecosystem model. Finally, a summary of the work is presented in Chapter 6, as well as suggestions for future work.

1.1 Objectives of this study

This study aims to better understand species interactions in the Antarctic through developing and extending multispecies models of the system. The models developed build on the model developed by Mori and Butterworth (2006). Their model included six predators: blue whale *Balaenoptera musculus*, fin whale *B. physalus*, humpback whale *Megaptera novaeangliae*, minke whale *B. bonaerensis*, Antarctic fur seal *Arctocephalus gazella* and crabeater seal *Lobodon carcinophagus*, and one prey species, krill (*Euphausia superba*). Krill is the dominant prey item of all these whales and seals. Harvesting (to near extinction) of the large baleen whales (blue, humpback and fin whales) from the start of the 20th century led to a likely increase in the availability of krill to other krill predators such as the Antarctic minke whale and crabeater seals (Mori and Butterworth, 2006). This phenomenon is referred to as the “krill surplus” hypothesis (Laws 1977) and has been a central hypothesis of Antarctic ecosystem studies.

The aim of the Mori-Butterworth model was to explore whether predator-prey interactions alone, without including environmental changes, could broadly provide an explanation of observed predator population trends since the onset of fur seal harvests in 1780. Mori and Butterworth obtained a reasonable fit to existing population abundance and trend estimates for the Atlantic/Indian and Pacific regions. However, one limitation of their approach is that all the whale and seal species considered have relatively slow dynamics, whereas faster reproducing species such as fish and squid may instead have taken primary advantage of any krill surplus and hence increased in abundance. Furthermore, their model gave a surprising result for fin whales. About 700 000 fin whales were caught in the Southern Hemisphere during the last century, more than from any other large whale population. However the Mori-Butterworth model suggests there were originally only about 200 000 fin whales, far fewer than indicated by models without species interactions, because (according to their model) fin whales were able to benefit from extra krill made available by the over-harvesting of humpback and blue whales which occurred before the fin whales themselves were heavily reduced by overharvesting. This study therefore addresses two questions:

(1) What independent evidence is there to support the low estimates of original abundance for Southern Hemisphere fin whales that are suggested by the Mori-Butterworth model?

(2) What is the impact of introducing a further predator with fast dynamics, such as squid, in the Mori-Butterworth Antarctic ecosystem model?

The methods which will be used to address these two questions are:

I. Develop a simple model for fin whales and their interaction with other species.

II. Extend the Mori-Butterworth Antarctic ecosystem model by adding squid as an example of predator with fast dynamics.

In what follows, the various multispecies modelling approaches are reviewed to provide a context to the study.

1.2 Multispecies models

1.2.1 General overview of multispecies models.

Fisheries multispecies models are defined here as models that include inter-specific interactions to assess the ecosystem effects of fishing via the biological relationships between species. Such models may vary in complexity (such as the number of parameters that need to be estimated) depending on the data available. More complex models require more estimable parameters, which lowers the precision of estimates and hence the predictive power of the model. There are many different types of multispecies model, as summarized in Plaganyi (2007). These include, for example, dynamic multispecies models (for example MSVPA, MSFOR, MULTSPEC, IBM, MSM, GADGET and BORMICON), aggregate system models (for example ECOPATH, ECOSIM, and ECOSPACE) and dynamic system models (for example IBM, OSMOSE, IGBEM and ATLANTIS). Multispecies models can be used to evaluate the impacts of fishing in marine ecosystems such as direct and/or indirect mortality of the target or non target species. For example Hollowed *et al*. (2000) explain that predation (consumer control), competition (resource control) and environmental disturbance are the fundamental processes structuring ecological systems, and most multispecies models address only a subset of these factors. The following subsections briefly outline the different types of models and their applications. More detailed descriptions of model formulations are beyond the scope of this thesis.

1.2.2 Dynamic multispecies models

A dynamic multispecies model (which considers predator-prey interactions), aims to quantify the trophic interactions between a subset of the species in the ecosystem and to predict the consequences of these interactions. Here a brief review of some of the approaches with most relevance to this study is provided.

MULTSPEC (Multispecies model for the Barents Sea) is a multispecies forward simulation model which is structured into area, age and length (Tjelmeland and Bogstad, 1998). Bogstad *et al*. (1997) used MULTSPEC to model fish and marine mammals in the Barents Sea by quantifying the predation by marine mammals on fish. This spatially structured model simulated the age and size of harp seals, minke whales, cod, capelin, herring and polar cod. Bogstad *et al*. (1997) investigated the sensitivity of the model to stock sizes and food preferences of marine mammals, which do not react to changes in prey availability in the model.

MSVPA (Multi-Species Virtual Population Analysis) is an age-structured model in which fishing and predation mortalities are taken into account (Sparre, 1991; Magnusson, 1995).

GADGET (Globally applicable Area-Disaggregated General Ecosystem Toolbox) (http://www.hafro.is/gadget; Coordinator G. Stefansson) is an age, length or age-length structured statistical modelling approach which can be used to create a forward projection and simulation model of marine ecosystems. It is a powerful and flexible framework in which populations can be split by species, size classes, age groups, areas and time steps (Plaganyi, 2007). All these models (MULTSPEC, MSVPA and GADGET) have been used in fish population studies and fish stock assessment, and to inform fisheries management in many parts of the world, including the North Sea, Baltic Sea, Barents Sea, Bering Sea, Georges Bank, and Benguela Current System (Begley and Howell, 2004; Xiao, 2007).

Jurado-Molina *et al*. (2005) used a Multispecies Statistical Model (MSM) to estimate cannibalism within an age-structured model for the Chilean hake. The model was fitted to the total annual catch, acoustic biomass survey and length composition data from the fishery. In their model they considered the natural mortality of the juvenile age classes as a dynamic function of predation mortality. In general MSM allows the estimation of predation mortality at age as a measure of indirect effects of fishing (Jurado-Molina *et al.*, 2005). It also estimates parameters on a statistical basis, considers uncertainty, and projects population trajectories over a specified time frame (Jurado-Molina *et al.*, 2005; Plaganyi, 2007).

1.2.3 Aggregate system models

Aggregate system models are derived from food webs and energy budgets. For example ECOPATH is a mass-balance model which assumes linear trophic interactions (Polovina, 1984; Gasalla and Ross-Wongtschowski 2004). It is the most widely used approach for structuring dynamic models of exploited ecosystems. ECOSIM is a dynamic ecosystem model which can be used to simulate time dynamics under different harvesting scenarios (Walters *et al*., 2000; Christensen and Walters, 2004; Vidal and Pauly, 2004).

1.2.4 Minimum Realistic Model

The term Minimum Realistic Model (MRM) was first coined with reference to a model by Punt and Butterworth (1995) to investigate the impacts of Cape fur seals on two species of hake *Merluccius capensis and M. paradoxus*. *M. capensis and M. paradoxus* are found in shallow- and deep-water respectively. The MRM approach was developed as a follow-up to the workshop held in Cape Town in 1991 on responsible management of fur seals off the west coast of South Africa. . Predators included in the model were estimated to account for more than 90% of all mortality of hake. These predators are seals, large fish and the hake fishery. The model is age-disaggregated with half year time steps and it includes both cannibalism and interspecific predation. In general, the important advantage of MRM is that it restricts a model to those species most likely to have important interactions with the species of interest (Plaganyi 2007).

1.2.5 Summary

The models described above range from those that represent the whole ecosystem, termed whole ecosystem models (for example ECOPATH/ECOSIM and ATLANTIS) to those that consider only a few species in the ecosystem, termed Minimum Realistic Models (MRMs) (for example MSVPA, MSFOR, MULTSPEC, and GADGET) (Plaganyi, 2007). Whole ecosystem models include most of the ecosystem components including the lower trophic level and primary producer groups (Fulton *et al*., 2005; Plaganyi, 2007). Models of predation may be further classified as either 'efficient' or 'hungry' predator models (Butterworth and Plaganyi, 2004). In 'efficient' models (for example MSVPA, MULTSPEC) predators are assumed to always get their daily ration whereas in 'hungry' models predators are assumed to compete for a limited number of prey (for example ECOSIM). Furthermore, models may represent the effect of fishing only on the population of interest, the effect of a non target species on a commercial prey species (for example MSVPA and BORMICON) or effects operating in both directions (for example ECOSIM) (Plaganyi, 2007). Differences in data quality influence and limit the reliability of any analyses performed using these models.

The following Chapter reviews one particular ecosystem model, the Mori-Butterworth Antarctic ecosystem model, which was chosen because it is simple, pragmatic and self-consistent (Plaganyi, 2007). This model represents only a subset of the ecosystem and focuses on inter-specific interactions.

2 Mori-Butterworth Antarctic ecosystem model

The aim of the Mori and Butterworth (2006) Antarctic ecosystem model was to explore whether predator-prey and inter-species interactions alone, without including environmental disturbance, could explain observed predator population trends since the onset of harvesting starting with fur seals in 1780 (as stated in the objectives). They developed two versions of the model. In the first version two baleen whale species (blue and minke) were considered as predators with krill as prey (Mori and Butterworth, 2004). In the second version (2006 version), two further whale (fin and humpback) and two seal species: Antarctic fur and crabeater seals were included to increase the realism of the model and its ability to fit to the observed trends.

The area investigated by Mori and Butterworth was divided into two sectors (Figure 2.1): the Atlantic/Indian region (which they termed Region A), corresponding to International Whaling Commission (IWC) Areas II, III and IV (60°W – 120°E), and the Pacific region (Region P), corresponding to Areas V, VI and I (120°E – 60°W). Region A shows major changes in the abundance of whales and seals (Mori and Butterworth, 2006). The equations of prey and predator dynamics (Mori and Butterworth, 2006) are represented respectively by:

$$B^{a}_{y+1} = B^{a}_{y} + r^{a} B^{a}_{y}\left(1-\frac{B^{a}_{y}}{K_{a}}\right) - \sum_{j}\frac{\lambda^{j}\left(B^{a}_{y}\right)^{n} N^{j,a}_{y}}{\left(B^{j,a}\right)^{n}+\left(B^{a}_{y}\right)^{n}} \tag{2.1}$$

and

$$N^{j,a}_{y+1} = N^{j,a}_{y} + \frac{\mu^{j} N^{j,a}_{y}\left(B^{a}_{y}\right)^{n}}{\left(B^{j,a}\right)^{n}+\left(B^{a}_{y}\right)^{n}} - M^{j} N^{j,a}_{y} - \eta^{j,a}(N^{j,a}_{y})^{2} - C^{j,a}_{y} \tag{2.2}$$

where:

B^{a}_{y} is the biomass of krill in region *a* and year *y*; r^{a} is the intrinsic growth rate of krill in region *a*;

K_{a} is the carrying capacity of krill (in the absence of predators) in region *a*;

λ^{j} is the maximum per capita annual consumption rate of krill (in tons) by predator species *j* (where *j* represents either *b* (blue whale), *m* (minke whale), *h* (humpback whale), *f* (fin whale), *s* (Antarctic fur seals), or *c* (crabeater seals));

$N_y^{j,a}$ is the number of predator species *j* in region *a* in year *y*;

$B^{j,a}$ is the krill biomass when the per-capita consumption and hence also birth rate of species j in region *a* drops to half of its maximum;

μ^j is the maximum annual birth rate of predator species *j* (which can be considered to include calf-survival rate, as usually only the net effect of these two processes in combination is measurable);

M^j is the annual natural mortality rate of predator species *j* in the limit of low population size;

$\eta^{j,a}$ is a parameter governing the density dependence of natural mortality and/or birth (and calf survival) rate for predator species *j* in region *a*;

n is a parameter that controls whether a Type II or Type III functional response is assumed ($n = 1$ for Type II and $n = 2$ for Type III); and

$C_y^{j,a}$ is the catch of predator species *j* in region *a* in year *y*.

The model was fitted to data for predator abundance and trends and the parameters such as M^j, $N_{1780}^{j,a}, \lambda^j$, μ^j and r^a were estimated by minimizing the negative log-likelihood function (see Appendix 5.2 for more details). All species were assumed to be at equilibrium in 1780. An intra-specific density-dependence parameter (η) was added to allow a non-trivial coexistence equilibrium of the species considered. These terms essentially reflect the impact of limitations of breeding sites for seals, and intra-species competition effects for whales (Mori and Butterworth, 2006).

The main findings of the Mori-Butterworth model

- Laws' (1977) krill surplus hypothesis estimated a surplus of some 150 million tons of krill made available by the reduction of large baleen whales through overharvesting, but the result of the Mori-Butterworth Antarctic ecosystem model suggests that this value may be too high.
- The initial fin whale numbers are estimated to have been about the same as blue whales, despite the fact of the cumulative fin whale catch having been about twice as large.
- It is not sufficient to consider the interactions between the Antarctic baleen whales and krill alone. The major seal species, at least, need also to be taken into account

explicitly, and probably some other predator species in addition. It may, however, prove problematic to include squid in such a grouping, as it could evidence faster dynamics as a result of its higher maximum growth rate.

- There are differences in the historic dynamics of the Atlantic/Indian and Pacific regions, with appreciable changes in abundance in the former. The latter has been relatively stable by comparison.
- Crabeater seals appear to play a key role in the dynamics of the system (though this may in part reflect the model "using" them also as a surrogate for other bird, squid and fish species not explicitly included)

Although the model is age-aggregated rather than age-structured, it can be used as a starting point for understanding trophic interactions when modelling other systems (Plaganyi, 2007).

Before detailing into the implementation of the Mori-Butterworth Antarctic ecosystem model and the fin whale historic abundance determination model, the background to the biology of selected species is summarized in the next Chapter in order to gain more insight into the issues listed above.

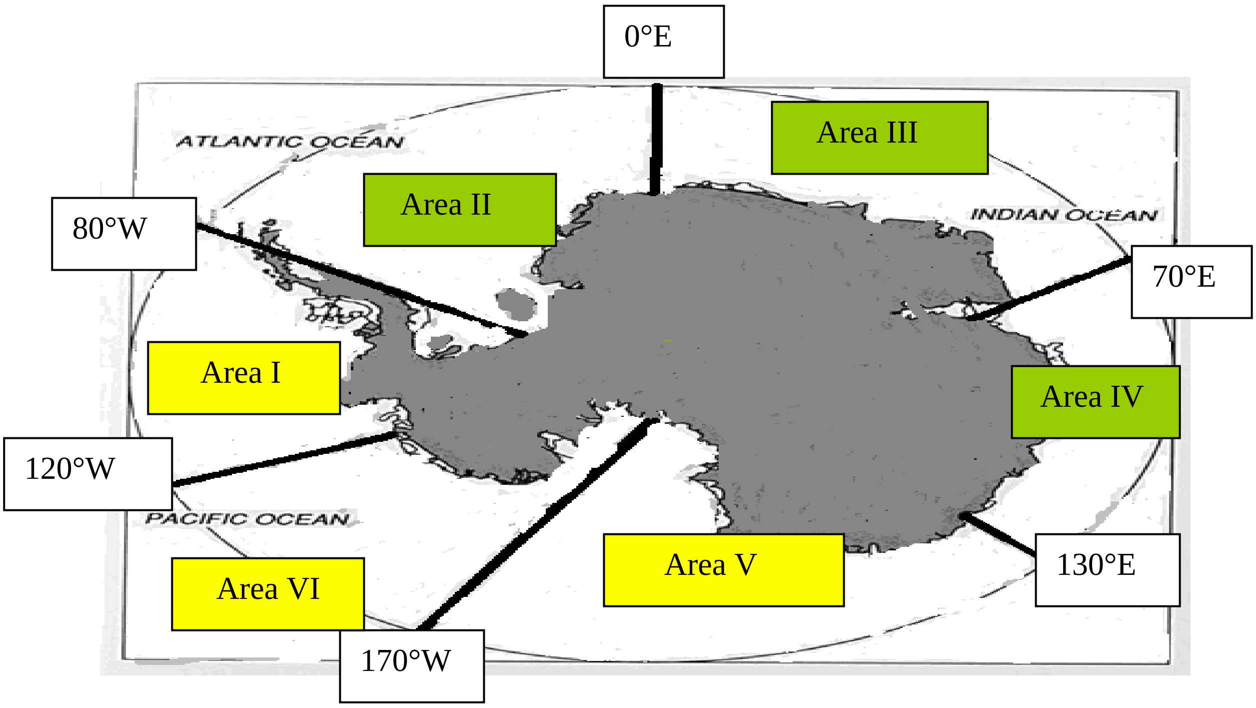

Figure 2.1: International Whaling Commission (IWC) management Areas. Areas II, III and IV represent Atlantic/Indian Ocean region while V, VI and I represent the Pacific Ocean region. For convenience the model refers to Areas II, III and IV as Region A whilst V, VI and I as Region P (source: aamap.jpg).

3 BACKGROUND TO SPECIES BIOLOGY

Aspects of the biology of selected Antarctic species included in the model are given below to provide a context for the study. The focus is on squid because this study adds squid to the original Mori-Butterworth Antarctic ecosystem model and the information obtained may assist in specifying realistic parameter values for squid dynamics both in the Antarctic and elsewhere. The term ‘squid’ in the Antarctic waters refers to this group of species in general, rather than a particular taxonomic family for squid.

3.1 Squid

Squid grow fast and typically have short life spans of not more than two years. They are sensitive to environmental conditions, both abiotic and biotic. These features make squid an interesting species for both theoretical and applied studies (e.g. Patterson, 1988; Basson *et al*., 1996; Roel and Butterworth, 2000; Ish *et al*., 2004; Bazzino *et al*., 2005; Miyahara *et al.,* 2006; Xinjuni *et al*., 2007). Squid spend the day near the bottom of the ocean, seeming to prefer areas where the bottom temperature is 6 to 7°C or greater (McMahon and Summers 1971; Phillips *et al*., 2001).

3.1.1 Feeding ecology

Short-lived fish typically display seasonal variation in their numbers and it seems likely that squid feeding habits are similarly subject to seasonal cycles (Ish *et al*., 2004). Most squid feed on krill and myctophids (Phillips *et a*l., 2001; Ish *et al*., 2004; Markaida, 2006). The extent of cannibalism among squid is unclear, but it would appear that the larger specimens are the most inclined to eat their own species (Coelho *et al*., 1997; Santos and Haimovic, 1997; Mouat *et al*., 2001; Vidal *et al*., 2006). The diet of squid is related to dorsal mantle length, with squid greater than 25cm consuming larger quantities of myctophids fish and smaller portions of cephalopods and crustaceans compared to smaller squid (Coelho *et al*., 1997; Santos and Haimovic, 1997; Mouat *et al*., 2001; Vidal *et al*., 2006).

Phillips *et al*. (2001) investigated squid *Moroteuthis ingens* around Macquarie and Heard Islands using 54 stomach contents (50 from Macquarie and 4 from Heard Island), using fatty acid composition to supplement these findings about their diet. They found that myctophid fish constitute 59% of the prey of *M. ingens* and consume 10% of their body weight per day. Stomachs collected near New Zealand have shown *M. ingens* prey on myctophid fish although others have suggested that squid feed on krill in the Southern Oceans (Phillips *et al.*, 2001). Phillips *et al*. (2001) report that the analysis of stomach content and fatty acid data did not show krill as a prey item of *M. ingens*. They suggest that the distribution of krill probably does not reach as far north as Macquarie and Heard Islands, and conclude that it is better to take the sample of squid from Antarctic waters where krill is distributed to reveal the squid diet by analyzing stomach contents.

Jackson *et al*. (2002) have shown that *Galiteuthis glacialis* lives in colder water where krill and its predators such as whales are found. *G. glacialis* feeds on krill. Shortfin squid, *Illex argentinus*, feed in cold water and spawn in warmer areas in the Southwest Atlantic Ocean (SWAO) (Bazzino *et al*., 2005). Santos and Haimovici (1997) investigated the diet and feeding habits of shortfin squid off southern Brazil based on stomach contents of 729 juveniles, subadults, and adults caught with a trawl from 1981 to 1992 and concluded that they feed on myctophids fish (43.8%), cephalopods (27.5%) and crustaceans (18.7%). Myctophids fish species in the diet included *Diaphus dumerilii*, *Maurolicus*, and *Merluccius hubbsi*, the cephalopods are *I. argentinus*, *Loligo sanpaulensis*, *Spirula spirula*, *Semirossia tenera* and *Eledone gaucha* and the crustaceans are *Oncaea media* and various *Euphausia* spp. Mouat *et al*. (2001) examined shortfin squid collected in the Falkland Islands jigging fishery and found small individuals feed on crustaceans while large ones feed on myctophids fish (> 240 mm ML). These authors examined 640 stomach contents.

3.1.2 History of the squid fishery

Exploitation of squid worldwide has increased substantially over the last two decades, with a total world catch of 3 173 272 tons in 2002 (Pascual *et al*., 2005). According to the literature, there are different types of squid species in different areas of the Antarctic. A summary of commercially important squid from the Southern Hemisphere is given in the subsections below.

3.1.2.1 Jumbo (*Dosidicus gigas*) and the New Zealand (*Nototodarus*) squid

Dosidicus gigas supports a major fishery in the south east Pacific whilst the two species of *Nototodarus* (*N. gouldi* and *N. sloani*) support fisheries in the western Pacific. The catch of *Nototodarus* is highly variable, depending upon the survival rate of juvenile squid (Waluda *et al.*, 2004). So far about 190 000 tons of *D. gigas* in 1994 in the Southern Hemisphere (off Peru) have been harvested (Hatfield, 2000). This species exhibits large fluctuations in abundance from year to year. However, the natural fluctuations that occur in abundance and distribution of many squid species are, in most cases, still poorly understood.

3.1.2.2 Chokka squid (*Loligo vulgaris reynaudii*)

Most of the population of *Loligo vulgaris reynaudii* is associated with the Benguela/Agulhas current system and is fished off the south and west coasts of South Africa, at the confluence of the Atlantic and Indian Oceans, though the detailed movements of this species are still unknown. The directed fishery was developed in 1985. Prior to that these squid were mainly caught as a by-catch by demersal trawlers. The fishery for *L. reynaudii* varies considerably and has attained 10 000 tons per year. Catch rates during 1988/9 reached 9792 tons while in 1992 dropped to 2587 (Roberts and Sauer, 1994; Sauer *et al.*, 2000; Glazer and Butterworth, 2006). Studies from the south coast of Portugal show a total of 964 tons *L. reynaudii* were harvested between March 1993 and October 1994 whilst 848 tons were harvested between June 1993 and January 1994 in the Saharan Bank (Central-East Atlantic).

3.1.2.3 Shortfin squid (*Illex argentinus*)

Shortfin squid, *Illex argentinus* is a highly migratory species distributed off the Patagonian shelf and Falkland Islands (Waluda *et al.*, 2004). The fishery in the Southwest Atlantic is found at 45-48°S between January and May, with peak catch rates in the months of April and May. The catches of shortfin squid started around the late 1970s and increased around the mid 1980s, which led to the introduction of an Island Interim Conservation and Management Zone (FICZ) in October 1986 to control the fishing effort (Basson *et al.*, 1996; Bazzino *et al.*, 2005). Annual catches of this species attained 500 000-750 000 tons (Bazzino *et al.*, 2005).

3.1.3 Growth and natural mortality

The growth rate and natural mortality of squid in the Antarctic are not well known. Some researchers have found that growth and natural mortality of squid vary seasonally. For example Basson *et al*. (1996) estimated the natural mortality of shortfin squid to be 1.44 per year for the period December to June and 2.88 per year for July to November. The range of their mortality values was from 0.96-4.8 per year and suggested that a mortality rate higher than 4.8 per year may be unrealistic. Roel and Butterworth (2000) suggested that the annual mortality rate of squid *L. reynaudii* is in the range of 1-2. They argue that less than 1 or greater than 2 per year is unrealistic. It seems that a value of about 2 per year would be compatible with the suggestion of both Basson *et al*. (1996) and Roel and Butterworth (2000).

Summers (1971) investigated the growth rate of *Loligo pealei* and suggested that they likely have a fast growth rate. Hanlon *et al*. (1983) suggest that the growth rate of squid can be temperature dependent, given that *L. pealei* grow faster at high temperatures. On the other hand, Patterson *et al*. (1988) suggested that the growth rate of *L. gahi* appear to vary less with a change in temperature. Others (for example Roberts 2005; Roberts and Sauer 1994) have noted similarity in life history aspects between *L. pealei* and *L. vulgaris* and this certainly extends to their age and growth rate, but their intrinsic rate of increase is still unknown.

3.1.4 Biomass of squid

The current biomass of squid in the Antarctic is not well known. During the BROKE survey in 1996, Jackson *et al*. (2002) found that in the Weddell Sea (located in the South Atlantic) *G. glacialis* was the most abundant squid species and suggested that the biomass of squid was 100 million tons, i.e. of the order of total worldwide catches of marine fish species. However, o reliable data exist on the total squid population, its biomass, or its distribution because of sampling difficulties.

3.2 General review of baleen whales, seals and krill in the Southern Hemisphere.

The Southern Hemisphere baleen whale populations are comprised of several species. Six of them are found south of the Antarctic Convergence: the blue, fin, sei, minke, humpback and southern right whale (*Eubalaena australis*). Studies have shown that these whales migrate between low latitude breeding grounds during the southern winter and high latitude feeding grounds during the southern summer. As part of its comprehensive assessment of all whale stocks, the International Whaling Commission (IWC) has identified some southern baleen whales as showing some signs of recovery after being reduced to very low levels prior to protection in the mid-1960's. However, generally these whale stocks remain at low levels.

Among the seals found in the Southern Ocean, crabeater seals are considered to be a true Antarctic seal species and comprise two-thirds of the world's seal population (Priddle *et al*., 1998). Their life-cycle is associated with ice-zones. Antarctic fur seals are rarely found in areas of pack-ice and inhabit pelagic regions in lower latitudes. They breed on Subantarctic islands.

Krill are found in the Antarctic waters of the Southern ocean. They have a circumpolar distribution with the highest concentrations located in the Atlantic sector and are key species in the Antarctic ecosystem (Phillips *et al*., 2001; Lawson *et al*., 2008). There are more than 80 recognized species of krill in the world oceans, including several different species that live in Antarctic waters. One species of Antarctic krill, *E. superba*, is the most abundant species in the Antarctic. In Ross Sea *E.crystallorophias* is the most abundant species, however. These species feed predominantly on phytoplankton. The value for the density of krill (*E. superba*) in the Indian Ocean has been estimated to vary from 6 to 305 mg/1000 m^3 (Ingole and Palulekar, 1993). The biomass of krill in the South Shetlands is estimated to be between 0.2 to 1.5 million tons (Ichii *et al*., 1994).

3.2.1 Baleen whales, seals and the krill fishery

The seal and baleen whale fisheries were the largest fisheries in the Southern Ocean in the 18th -19th and the 20th centuries respectively. Some of these species have been reduced to near extinction (Branch *et al*., 2004; Clapham *et al*., 1999; Mori and Butterworth, 2006). In South Georgia, about 1.2 million Antarctic fur seals were removed by 1822, followed by the South Shetland Islands by 1830 (based on Mori and Butterworth, 2006 – citing in Weddell, 1825). It has been estimated that over 360 000 blue and 725 000 fin whales were harvested from the Southern Hemisphere during the 20th century (Branch *et al*., 2004; Sirovic *et al*., 2004). Branch *et al*. (2004) mention the areas in the Antarctic where large and small catches of blue whales took place. The commercial harvest of humpback whales reduced this species to 1–5% of their estimated pre-exploitation abundance (Johnston and Butterworth, 2005a,b).

In contrast, among baleen whales included in the model, minke whales were harvested to a lesser extent and their exploitation started only in the 1970's (Mori and Butterworth, 2006).

After over-exploitation of seals and whales, attention moved down the food web to begin exploitation of fish and krill from the late 1960's onwards. The commercial fishery for krill started in the 1972/1973 season by the Soviet and Japanese fleets and peaked in 1981/1982 (Agnew, 1997). The main fishing grounds are to the east of South Georgia, the Prydz Bay area, around the South Orkney Islands and Antarctic Peninsula, off the north coast of the South Shetland Islands and between Prydz Bay and the Ross Sea (Agnew, 1997; CCAMLR, 2002) (Figure 3.1). Originally an annual sustainable catch of more than 150 million tons of krill was postulated representing the so-called "krill surplus" caused by the great reduction in baleen whale stocks (Laws' 1977). The catch limit for krill has been set at 4 million tons in CCAMLR Area 48, but recent annual catches are only 90 000 to 160 000 tons (Agnew, 1997; CCAMLR XXIII, 2004; Hewitt *et al.*, 2004; Gross, 2005).

Despite the fact that baleen whales were harvested close to extinction there is evidence for recovery in some of the species since their harvesting ceased. For example, Branch *et al.* 2004 used a Bayesian approach to estimate the recent rate of increase of blue whales, which they found to be 7.3% per annum. Along the west coast of Australia, humpback whales increased at about 10.9% per annum from 1963 to 1991 (Bannister, 1994) whilst a high rate of increase (at about 17.8%) in the abundance of fin whales in the Antarctic Areas IIIE (35°E–70°E) and IV (70°E–130°E) is reported by Matsuoka *et al.* (2005). These increases in some whale species, particularly fin and humpback whales, may be impeding the growth of others. For instance minke whale and crabeater seals that seem to have benefited from the hypothesized "krill surplus" may now be decreasing (Branch and Butterworth 2001a; Mori and Butterworth, 2006).

3.2.2 Krill as prey for whales and seals

In general, almost all species of Antarctic seals (crabeater, leopard *Hydrurga leptonix*, Ross *Ommatophoca ross*, Wedell *Leptonychotes wedelli*, and Antarctic fur seals) and most of the large whale species (i.e. blue, fin, minke and humpback whales) are important consumers of krill (Green and William, 1988; Agnew, 1997; Boyd and Murray, 2001; Kock, 2005). The differences in the annual amount of krill taken differ between species and location (Lowry *et al.*, 1988; Pauly *et al.*, 1998; Mori and Butterworth, 2006). For example, Pauly *et al.* (1998)

estimated the proportion of krill in the diet of crabeater seals to be 90%, Antarctic fur seals 50%, fin whale 80%, blue whale 100%, minke whale 65% and humpback whale 55%. These figures are similar to those assumed by Mori and Butterworth (2006) for their estimated "Reference case" model: 50% for fin whales, 60% for Antarctic fur seals, 94% for crabeater seals and 100% for blue, minke and humpback whales. Murase *et al*. (2002) investigated the relationship between the distribution of krill and baleen whales in the Antarctic (35°E–135°W) using hydroacoustic and sighting surveys respectively. These surveys were conducted over the period 1998 to 2000. Generally his study shows that high concentrations of baleen whales (such as blue, fin, humpback and minke whale) are correlated with large aggregations of krill along the ice edge, further strengthening the argument that these whales feed primarily on krill.

3.3 Historical catches and ecology of some Antarctic species not included in the model

Icefish and Patagonian toothfish

The Antarctic contains a peculiar group of fish called the icefish. These vertebrates lack haemoglobin in their blood. The fish are also fast growing and short lived. They complete their life cycle in about one year (Kock *et al*., 1985). Among the three species of icefish (*Champsocephalus aceratus, C. rhinoceratus*, and *Pseudochaenichthys georgianus*), mackerel icefish *C. gunnari* have a widespread distribution in both the Atlantic (South Georgia, Bouvet Island, South Sandwich, South Orkney, South Shetland Island and the northern part of the Antarctic Peninsula) and Indian (Shelf off Kerguelen Island, Skif shoal West of Kerguelen Island and on the shoal between Kerguelen and Heard Island) Oceans (Figure 3.1) (Everson, 1992; Kock, 2005; Kock and Everson, 1997; La Mesa and Ashford, 2008). The wide distribution and dense concentrations of icefish favor fishing operations. As a result, *C. gunnari* was heavily exploited from the beginning of the 1970's to 1990. Annual catches exceeded 100 000 tons in some years (Kock and Everson, 1997; Constable *et al*., 2000).

The Patagonian toothfish *Dissostichus eleginoides* plays an important part in the Southern Ocean ecosystem around Antarctica (De la Rosa *et al*., 1997). Fishing for this species started around South Georgia (Figure 3.1) in the 1970's when illegal catches were estimated to be 4 to 12 times the legal limit, or greater (Agnew, 2000; Constable *et al*., 2000). In 1996/1997 the pressure from illegal (taken in the Exclusive Economic Zone of a sovereign country), unreported (when taken by CCAMLR members but not reported) and unregulated (when taken by non-members) fishing shifted to the Indian Ocean. In 1998/1999 the fishery around Prince Edward and Marion Islands was over fished to the point of commercial extinction, in just 1–2 years (Constable *et al.*, 2000).

Studies to date indicate that all icefish species in the Southern Ocean feed primarily on krill (Kock and Everson, 1997). Some species of icefish, for example *C. gunnari*, have been occasionally found in stomachs of Antarctic fur seals, black-browed and grey-headed albatross at South Georgia, such as in 1994, when krill was scarce (Constable *et al.*, 2000; Kock, 2005). De la Rosa *et al.* (1997) investigated the diet of Patagonian toothfish in two offshore regions in the southwestern Atlantic. They found that adultsfeed on fish, crustacean and cephalopods while juveniles feed on krill.

Icefish and Patagonian toothfish could have been used in this study, instead of squid, as examples of fast growing and short lived species. It is possible that these species would have been the first to benefit from any krill surplus after the reduction of whales to near extinction. This would allow more detailed investigation of their dynamics, but for this study squid was taken to be representative of all these species.

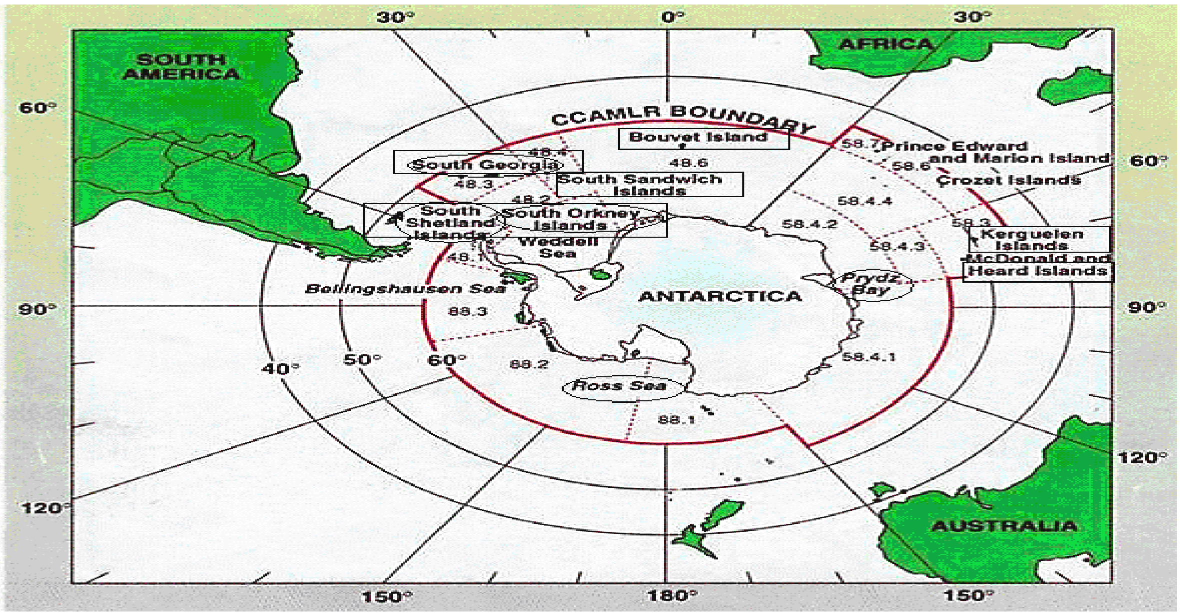

Figure 3.1: The main fishing grounds for krill (circled), icefish and Patagonian toothfish (triangles) in the Antarctica. (source: http_www.lighthouse-foundation.bmp)

4. FIN WHALE HISTORIC ABUNDANCE DETERMINATION MODEL

4.1 Introduction

Most historic catches in the Southern Hemisphere were on the Atlantic side of Antarctica. Given information about historic catches, population natural growth rates and current abundances, the pre-exploitation abundance of whale species before harvesting can be calculated. As mentioned in Chapter 1 the Mori-Butterworth Antarctic ecosystem model suggests that there were originally only about 200 000 fin whales, far fewer than estimates from models without species interactions. Therefore the pre-exploitation abundance for fin whales estimated by the Mori-Butterworth Antarctic ecosystem model has generated controversy as this result has both biological and management implications. If the pre-exploitation abundance of the population is over- or under-estimated, the level of recovery at any time will be correspondingly under- or over-estimated, and could lead to the resource being wasted, or a premature increase in pressure to resume hunting of a depleted population. It could also confound the interpretation of future responses of whale populations to environmental and other induced changes, such as global warming and overfishing by humans. Ecological changes could affect the carrying capacity, and could alter the dynamic response of recovering whale populations (Baker and Clapham, 2004).

The key question is whether the low Mori and Butterworth estimate is plausible and supported by independent evidence? One key line of evidence is to examine the catch per unit effort (CPUE) data for whaling off Durban on the east cost of East Africa in the middle decade of the last century. Models are applied to the whole of Region A (Atlantic and Indian Oceans) and to a subset of Region A, IWC Management Area III. The reasons for choosing Region A are:

a) there was a greater whale harvest in Region A, and therefore the impacts on the dynamics of these species are greater; and
b) Region A is the region to which the data from whaling off Durban corresponds.

The model is also applied to IWC Area III because it is uncertain how large an overall fin whale population is represented amongst fin whales taken off Durban, so they may relate only to this smaller region. The models applied to these two regions are used to assess the pre-exploitation abundance of fin whales.

4.2 Data

4.2.1 Catch data for fin and blue whales

Southern Hemisphere fin whale catches from IWC Management Area III and for Region A (Management Areas II + III + IV) south of 40°S were provided by C. Allison of the IWC Secretariat and north of 40°S by M. Mori (taken from information originally provided to her by C. Allison) (see Figure 2.1 which shows these Areas). In a few instances, assumptions had to be made for the position of southern catches where this information was lacking in the data. For example in 1909 total catches were 232 whales near Kerguelen. Among these whales, 6 were specified as fin whales and none unspecified, so the estimate of fin whales taken in area III was taken as 6 because Kerguelen is in Area III. Pelagic catches for fin whales, south of 40°S and of unknown position, in 1926-1929 were assumed not to be from Area III as there were no recorded pelagic catches in this Area until 1930. Uncertainty in the assumptions made should be minor (C. Allison, pers. commn). Catches from Area III are shown in Table 4.1 and catches from Region A are shown in Table 4.2.

Blue whale catches in the Atlantic/Indian Ocean and in Area III alone were taken from Rademeyer *et al*. (2003). These catches (both in Area III and Region A) are listed in Tables 4.1 and 4.2 respectively.

4.2.2 Commercial catch rates off Durban

CPUE data for fin and blue whales were taken from Best (2007). Best (2007) comments that: "Effort to catch whales was measured by the number of hours searching per month. Standardization of fishing effort data therefore depends on determining whether there are appreciable variations (especially trends) in effective fishing time, fishing power, or distribution of the fleet, and if so making the necessary standardization of the appropriate component of the total fishing effort. In these data an obvious seven-day periodicity in no catch days was evident, indicating that no whaling took place on Sundays. These plus all other days of no catch were considered as "non-productive" boat days and subtracted from the overall number of calendar days available for that month. This procedure could have under-estimated effort if there were days of search effort but no catch."

The localized *CPUE* provided by these data is assumed to be proportional to whale abundance in the analyses that follow. Note that the effort used to calculate CPUE was non-directed, i.e. was not the effort expected to have been actually spent targeting these species hence the *CPUE* data are non-directed, which could mean that *CPUE* is not reliable index of abundance. As detailed by Biseau (1998), directed CPUE[1] seems to be a more robust index of abundance than total *CPUE* (i.e. that based on directed + non-directed trips). These *CPUE* data consist of separate series for blue whales for which catch rates are available for 1920, 1922-1928 and then from 1954 to 1975, whilst for fin whales data are available for 1920, 1922-1926, 1928 and then from 1954 to 1975 (see Table 4.3). For the 1920s, catch and effort data are available over April-December, whereas the 1950s-1970s data are available over February-October. For comparability over time the *CPUE* in year y was calculated by using the data from the May-September period (for 1920s as well as 1950s-1970s) and is given by the following formula:

$$CPUE_y = \frac{\sum_{i=May}^{September} Catches_y}{\sum_{i=May}^{September} Effort_y} \tag{4.1}$$

4.3 Estimates of abundance from surveys by Region or Area

The abundance estimates for Region A for fin and blue whales used by Mori and Butterworth (2006) were taken from Branch and Butterworth (2001b). The abundance estimates for Area III only which are used here, were derived from the information provided in Branch and Butterworth (2001b). Note that Branch and Butterworth estimate abundance from a survey using the equation:

$$P = \frac{nA\bar{s}}{2Lw} \tag{4.2}$$

where

- P is uncorrected abundance (assumes all schools on the track line are sighted and makes no correction for random school movements);
- n is the number of schools primary sighted;

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[1] The direct *CPUE* are *CPUE* which can be calculated from the catch realized when targeting one species and the associated effort.

- L is the primary search effort;
- w is effective search half-width for schools;
- $\bar{s}$ is the estimated mean school size; and
- A is the area of the surveyed strata.

For each of fin and blue whales, common values of $\bar{s}$ and w were used for the different Areas because the sample sizes to estimate these are small. From this it follows that abundances by Area are proportional to $\frac{nA}{L}$ and hence (since Region A comprises Areas II, III and IV) that for fin whales:

$$F_{III} = \frac{\frac{n_{III}^{f} A_{III}}{L_{III}} \sum_{i=II}^{IV} F_i}{\sum_{i=II}^{IV} \frac{n_i^{f} A_i}{L_i}} \tag{4.3}$$

and for blue whales:

$$B_{III} = \frac{\frac{n_{III}^{b} A_{III}}{L_{III}} \sum_{i=II}^{IV} B_i}{\sum_{i=II}^{IV} \frac{n_i^{b} A_i}{L_i}} \tag{4.4}$$

where

- F_i and B_i are the survey abundance estimates for fin and blue whales in area i where i =II, III or IV. (Note that $\sum_{i=II}^{IV} F_i$ and $\sum_{i=II}^{IV} B_i$ are provided in Mori and Butterworth (2006).)

The abundance estimates that result for Area III, together with the estimates for Region A from which they are derived, are shown in Table 4.4. There are some uncertainties associated with abundance estimate for Region A. This is because the abundance estimates are based on survey data south of 60°S, but fin whales spend some of their time further north. Possibly therefore these estimates may not reflect the current total population size of fin whales. For example, Ensor *et al*. (2006) found that on the 2005/06 IDCR/SOWER survey of the region from 55-61°S and 5-20°E north, there were 31 groups of 274 individual fin whales sighted. This is more than were sighted during any complete survey by two to three cruise vessels involved over a much longer time period south of 60°S during 1978-1997. Note that Mori and Butterworth (2006) extrapolated the abundance estimate for fin whales by a factor of seven as the previous estimate from Butterworth and Geromont (1995) estimated abundance for the area south of 30°S. Uncertainty in the blue whale abundance estimates should be minor by comparison (T. Branch, pers. commn).

4.4 Models developed

In this section, two models are used to estimate pre-exploitation abundance from the data. The models are simple because the data available are limited, and differ in the way that the growth rate of one species is affected by the presence of the other.

In both instances, per capita growth rate decreases both with increasing abundance of the species concerned (density dependence) and with increasing numbers of the competitor species. The way these two effects inter-relate is however different. In model GR_1, per capita growth rate drops as the competitor species increases in abundance even as the abundance of the species concerned approaches zero (Figure 4.1), whereas in model GR_2, the species concerned can maintain a maximum per capita growth rate at low abundance irrespective of the abundance of the competitor species (Figure 4.2).

The quantitative differences between models GR_1 and GR_2 can be also described in the context of the “basin” model (MacCall, 1990). The “basin” model relates habitat suitability to the intrinsic rate of population growth and to population size as a function of the local carrying capacity of the habitat. MacCall argued that as population numbers decrease, there should be a contraction of the population range to optimal habitats whereas when populations numbers increase, the population expands into marginal habitats. This is also supported by Simpson and Walsh (2004) who explore the spatial-temporal variation in the distribution of yellowtail flounder on the Grand Bank to test MacCall’s basin hypothesis.

The basin model explains why, when there is a competitor (or poor environmental conditions), one might expect the growth rate and the carrying capacity (*K*) to decline (GR_1), instead of the carrying capacity alone (GR_2). In other words, as the availability of preferred habitats decline, fish (or whales) begin to occupy less suitable habitats and this would affect their growth rate negatively.

4.4.1 Model GR_1[2]

The dynamics of fin whales are given by:

$$F_{t+1} = F_t + \frac{r_f F_t}{K_f}\ (K_f - \alpha B_t - F_t\ ) \text{ - } C_t^f : \qquad (4.5)$$

and the dynamics of blue whales by:

$$B_{t+1} = B_t + \frac{r_b B_t}{K_b}\ (K_b - \beta F_t - B_t\ ) \text{ - } C_t^b : \qquad (4.6)$$

where

- F_t and B_t are the number of fin and blue whales respectively at the start of the year *t*;
- r_f and r_b are the intrinsic (maximum per capita) growth rates of fin and blue whales respectively;
- K_f and K_b are the carrying capacity or unexploited equilibrium level for fin and blue whales respectively, each in the absence of the other;
- α and β are the interaction (competition) terms for blue and fin whales respectively; and
- C_t^f and C_t^b are the annual catches for fin and blue whales respectively.

In this model one would expect α and β to be proportional to the annual consumption rates of krill by individual blue and fin whales respectively, for which Mori and Butterworth (2006) provide the values of λ_b (=450 tons) and λ_f (=110 tons). Note that for one extra fin whale, K_b decreases by β and for one extra blue whale K_f decreases by α. Therefore the relationship between the ratios of α to β and of λ_b to λ_f would be expected to be:

$$\alpha : \beta = \lambda_b : \lambda_f \qquad (4.7)$$

This implies that (approximately) $\beta = \frac{1}{4}\alpha$. Further, in order to satisfy the condition for stable mutual co-existence equilibrium $\alpha\beta < 1$ (see Appendix 4.1 for a derivation of this result).

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[2] GR_1 is an abbreviation for Growth Rate 1

From these two relations it follows that the value of α must be less than 2. Thus when implementing this model, the values of α were chosen within the range of [0, 2).

4.4.2 Model GR_2[3]

The dynamics of fin whales are given by:

$$F_{t+1} = F_t + r_f F_t (1 - \frac{F_t}{K_f - \alpha B_t}) - C_t^f \tag{4.8}$$

and the dynamics of blue whales by:

$$B_{t+1} = B_t + r_b B_t (1 - \frac{B_t}{K_b - \beta F_t}) - C_t^b \tag{4.9}$$

The values for α and β are set using the relationship above ($\alpha\beta < 1$) in order to satisfy the condition for stable mutual co-existence (see Appendix 4.1). Therefore, the values of α examined were selected from the same range as in Model GR_1.

4.5 Fitting the model to the data

The model has 5 unknown parameters (K_f, K_b, r_f, r_b and α), but with only two data points in the form of recent estimates of abundance for the two species. Results are therefore obtained by first assuming certain values for r_f, r_b and α, and then calculating the values of K_f and K_b which yield population trajectories passing through the values of recent abundance for the years to which they refer, where these trajectories are computed using equations 4.6 and 4.7 for model GR_1 and equations 4.8 and 4.9 for model GR_2. The condition that fin and blue whales were in equilibrium ($F_{t+1} = F_t = F_o$ and $B_{t+1} = B_t = B_o$) prior to catches yields from equations (4.6) to (4.9):

$$K_f = F_o + \alpha B_o \tag{4.10}$$

$$K_b = B_o + \beta F_o \tag{4.11}$$

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[3] GR_2 is an abbreviation for Growth Rate 2

In order to calculate unexploited equilibrium level for fin (K_f) and for blue whale (K_b) in the absence of the other, the initial populations of each species before exploitation (F_o and B_o in year t=0) need to be obtained. The simplest way to solve these non-linear equations for the two unknowns (K_f and K_b) is by a non-linear minimization process to achieve a zero value for the function:

$$S(K_f, K_b) = (F_{obs(1997)} - F_{\mathrm{mod}\,el(1997)})^2 + (B_{obs(2000)} - B_{\mathrm{mod}\,el(2000)})^2 \qquad (4.12)$$

where

- $S(K_f, K_b)$ represents the sum of squares function to be minimized;
- $F_{obs(1997)}$ is the fin whale survey abundance estimate in 1997;
- $F_{\mathrm{mod}\,el(1997)}$ the fin whale model (for example GR_1) abundance in 1997;
- $B_{obs(2000)}$ is the blue whale survey abundance estimate in 2000; and
- $B_{\mathrm{mod}\,el(2000)}$ is the blue whale model abundance in 2000.

The value of r_f was taken to be 0.126, being the maximum demographically achievable as suggested by Brandao and Butterworth (2006) (here the growth rate of fin whales is assumed to be approximately the same as this maximum demographically possible growth rate of humpback whales). Blue whales in the Antarctic are still at low population sizes so may be expected to be growing at close to their maximum rate. The growth rate estimate of Branch *et al.* (2004) of 7% is thus similar to the value for r_b which is assumed here for simplicity to be equal to 0.5 r_f that is 0.063.

Given survey abundance estimates (for fin and blue whales in 1997 and 2000 respectively), values for r_f and r_b and time series of catches for fin and blue whales for Area III and for the Atlantic/Indian region (Tables 4.1 and 4.2 respectively), the values of the parameters K_f and K_b were calculated by minimizing the $S(K_f, K_b)$ using AD Model Builder™. The possible pre-exploitation abundances (F_o and B_o) were evaluated considering both the absence of competition (i.e. $\alpha = \beta = 0$) and at various levels of competition (i.e.

$\alpha \neq \beta \neq 0$). It turns out that model GR_1 and GR_2 give similar estimates of K_f, K_b, F_o and B_o the same values of α are input (see Table 4.5).

4.6 Calibrations for the number of fin and blue whales off Durban

To compare model predictions of whale numbers to the Durban CPUE a constant of proportionality is needed. This is estimated from the ratio of average model numbers to average CPUE over a period where both are available. The period chosen for this standardization was 1954 to 1970 because continuous data are available for this period; thus numbers for fin and blue whales off Durban suggested by the CPUE data were calculated using the following equation:

$$N^{D}_{j,t(\mathrm{Re}\,g.A/III)} = CPUE_{j,t} \times \frac{N^{av(1954-1970)}_{j,t(\mathrm{Re}\,g.A/III)}}{CPUE^{av(1954-1970)}_{j,t}} \qquad (4.13)$$

where

- $N^{D}_{j,t(\mathrm{Re}\,gA/III)}$ is the number of species *j* suggested by the *CPUE* trend off Durban for Region A or for Area III (*j* represents either fin or blue whales) in year *t*;
- $CPUE_{j,t}$ is the CPUE for species *j*;
- $N^{av(1954-1970)}_{j,t(\mathrm{Re}\,g.A/III)}$ is the average (over 1954-1970) number of species *j* on Region *A* or Area III indicated by the population model; and
- $CPUE^{av(1954-1970)}_{j,t}$ is the average (over 1954-1970) of CPUE for species *j*.

4.7 RESULTS

Blue and fin whale catches

In Region A commercial catches for blue whales increased during the 1920s, peaked in the 1930s, and then declined during the 1940s, with the last catch occurring in 1973. The fin whales followed with catches peaking in 1937 and again in the 1950s, and the last catches occurring in 1975 (see Figure 4.3). The patterns in Area III, after showing a later start than for Region A as a whole, are very similar to those for Region A. CPUE data for fin and blue whales off Durban are compared with the model trajectories (with CPUE treated as an index of abundance) in Table 4.3 and are plotted in Figure 4.4. CPUE for fin whales during the

1920s and 1970s is low compared to CPUE in the 1950/60s, suggesting lower abundance in the earlier period. This is opposite to blue whales for which CPUE in the 1920s is higher than CPUE from the 1950s to the 1960s.

Abundance trajectories for fin and blue whales

The results for models GR_1 and GR_2 are very similar, so that only those for model GR_2 have been plotted (see Table 4.5). This is even though model GR_2 can maintain maximum per capita growth rate of the species concerned at lower abundance regardless of the abundance of the competitor species (see their difference in Figures 4.1 and 4.2).

The effect of food/competition is shown by comparing the cases with and without interactions. Figure 4.5 shows the trajectories (for Region A) for blue and for fin whales without species competition compared to the Mori and Butterworth “Reference case” trajectory with inter-species interactions. The model developed hits the population estimates for the Atlantic/Indian region exactly (Figures 4.5 and 4.6) as intended for the K values calculated. Figures 4.6 (a) and (b) show the same results, but they are plotted differently to show the effect of interactions in (a) and compare the two species in (b). The fin (and blue) whale increases in the early 1940s are primarily because catches dropped during World War II (see Figure 4.6 (a)). Values of the model parameters (including estimates of the numbers of fin and blue whales for the initial year considered in this model, i.e. 1900) for the Region A and for Area III are given in Table 4.5. Trajectories for blue and fin whales (with interactions) in Region A are compared to CPUE data from the whaling off Durban in Figures 4.7.

Figure 4.8 shows the model developed hits the population estimates for Area III exactly as intended for K values calculated. The same Figure shows the calculated trajectories (with and without interactions) for fin and blue whales. Trajectories for blue and fin whales (with interactions) in Area III are compared to CPUE data from the whaling off Durban in Figure 4.9.

4.8 DISCUSSION

The Mori-Butterworth Antarctic ecosystem model suggests that the pre-exploitation abundance of fin whales was much lower than does the model without species interactions (Figure 4.5). This study investigates this further using a simpler model and based on the same data set for Region A as that used by Mori and Butterworth (2006). The simple model gives qualitatively similar results to the Mori-Butterworth Antarctic ecosystem model and these results are presented in Figures 4.6 (a) and (b). The model suggests that the population of blue whales was little affected (compare the trajectories with and without interactions in Figure 4.6 (a)), but in the presence of interactions fin whales start with lower abundance and stay almost stable until about 1950 when blue whales had already decreased to about 20% of their initial number (see Figure 4.6 (b) with interactions). Fin whale catches over the period 1920 – 1930 tend to decrease the fin whale populations but this is more than compensated by the increased prey availability as a result of the large decrease in blue whale numbers over this period (see Table 4.2 and model trajectories with interactions). Note that in Region A for the model with interactions, the fin whale abundance in the late 1940s is greater than its pre-exploitation size in 1990 because of the effect of the interaction terms. K_f depends on the number of blue whales This means that the decrease of number of blue whales led to the increase maximum possible reproduction of fin whales (see equation 4.8).

Figure 4.7 shows the model trajectories using data from Region A compared to available CPUE data from whaling that took place off Durban. This Figure shows that fin whale CPUE was higher in the 1960s than in the 1920s. The model trajectory compares reasonably to the fin whale indices in the 1950s and 1960s to which it has been calibrated (see equation 4.13), but is much higher than the corresponding CPUEs in the 1920s.

The model fits to the data in Area III are shown in Figure 4.8. Trajectories with and without interactions suggest that fin whales in Area III were always more numerous than blue whales. For both populations, there is only a small declining trend in model trajectories until the 1930s. This is due to the greater impact of harvesting of these species in other Areas (Areas II and IV) in Region A than in Area III over this period. There was a sharp decline for blue whales in Region A around the 1920s while in Area III this decline started only around the 1940’s (compare Figure 4.6 (a) and Figure 4.8 blue whale trajectories).

Figure 4.9 shows the model trajectories for Area III compared to CPUE data from whaling that took place off Durban. As for Figure 4.7, the model does not show broadly similar trends to the CPUE indices. The CPUE for blue whales for the 1960’s are very low. This overall lack of agreement may be because:

- The low values for blue whales in the 1960s are a genuine reflection of the fact that the population was very low over this period, or these data do not provide an adequate index of population abundance because they reflect only a small component of the population.

- The increase in fin whale CPUE in the 1950s compared to the 1920s may be due to technical changes (probably linked to technical improvements) or the CPUE for fin and blue whales are dependent. This means that it might be that blue whales were the target in the early period (1920s) and fin whales in the second period (1950/60s).

The reason for these different trends in the CPUE and model trajectories should be investigated further.

4.9 CONCLUSIONS

This Chapter set out to estimate the pre-exploitation abundance of fin whales by developing a simpler model and comparing results with those obtained by Mori and Butterworth (2006). To this end, the study used CPUE data from whaling off Durban as an independent data source providing an index of abundance, to check whether these data support the lower value suggested by the Mori-Butterworth Antarctic model.

The declining trend in CPUE observed for fin whales was much less rapid than for blue whales (Figure 4.4). The lower CPUE values in the 1920s suggest that fin whale populations were lower during these early years than during the later period around the 1960s. However, the blue whale CPUE series suggests higher abundance in the earlier period than in the later period around the 1950/1960s. The model trajectories compare reasonably to data from Region A and Area III to indices in the 1960s. Thus, in general, the results are compatible with the estimates obtained by the Mori-Butterworth Antarctic ecosystem model of a low pre-exploitation abundance of fin whales.

Results are similar whether one looks at Region A or Area III only. There are however important features of the CPUE that are not reflected by the model results, and a number of possible reasons are advanced for this. In particular regarding the increase in fin whale CPUE from 1920’s to the 1950’s which is not reflected by model trend, it may be that the two series are not comparable despite the efforts by Best to standardize these data. Even though the CPUE data for fin whales suggest a population increase, the closest manageable with a competition model is to maintain the fin whales abundance roughly constant (compare to a decrease without such competition) until about 1950.

Table 4.1: Historical catches from IWC Management Area III (north + south of 40°S). For fin whales data north of 40^o S are from M. Mori and south 40^o S from C. Allison, IWC, pers. commn. For blue whales data are from Rademeyer *et al.* (2003).

Catches from area III			Catches from area III		
Year	Blue whale	Fin whale	Year	Blue whale	Fin whale
1900	0	0	1955	386	14 267
1901	0	0	1956	313	8 496
1902[4]	0	0	1957	583	4 761
1903	0	0	1958	498	10 198
1904	0	0	1959	311	11 122
1905	0	0	1960	236	10 508
1906	0	0	1961	132	14 409
1907	0	0	1962	125	12 712
1908	0	2	1963	96	8 832
1909	4	7	1964	91	4 610
1910	8	4	1965	122	1 595
1911	52	61	1966	75	1 528
1912	126	187	1967	35	1 631
1913	438	1 037	1968	33	852
1914	825	802	1969	15	943
1915	665	901	1970	10	1528
1916	503	673	1971	7	1833
1917	545	476	1972	0	1151
1918	177	287	1973	0	619
1919	120	371	1974	0	445
1920	331	407	1975	0	19
1921	138	266	1976	0	0
1922	711	439	1977	0	0
1923	1 141	819	1978	0	0
1924	905	948	1979	0	0
1925	1 387	1 028	1980	0	0
1926	6 742	1 219	1981	0	0
1927	2 142	1 201	1982	0	0
1928	1 005	936	1983	0	0
1929	729	1 151	1984	0	0
1930	2 555	1 717	1985	0	0
1931	1 411	3 517	1986	0	0
1932	10 111	391	1987	0	0
1933	7 526	2 288	1988	0	0
1934	8 429	2 733	1989	0	0
1935	9 660	8 611	1990	0	0
1936	5 157	6 381	1991	0	0
1937	6 608	6 184	1992	0	0
1938	4 495	9 602	1993	0	0
1939	1 693	6 216	1994	0	0
1940	28	5 697	1995	0	0
1941	6	242	1996	0	0
1942	2	204	1997	0	0
1943	10	301	1998	0	0
1944	5	227	1999	0	0
1945	2 925	162	2000	0	0
1946	2 985	2 968	2001	0	0
1947	1 912	4 927	2002	0	0
1948	2 987	7 062			
1949	1 515	7 173			
1950	1 572	5 678			
1951	1 920	5 288			
1952	1 370	8 543			
1953	1 615	11 766			
1954	688	11 572	Total	98 947	244 731

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[4] Catches, for example in the split year 1902/03, in this study have been shown as for 1902.

Table 4.2: Historical catches in the Atlantic/Indian sector (Region A) for fin and blue whales considered in this study (sources as for Table 4.1).

Catches from Region A			Catches from Region A		
Year	Blue whale	Fin whale	Year	Blue whale	Fin whale
1900	0	0	1955	1 018	20 266
1901	0	0	1956	677	17 420
1902	0	0	1957	996	20 405
1903	0	0	1958	726	22 720
1904	11	4	1959	514	23 023
1905	51	104	1960	425	23 456
1906	68	133	1961	523	23 085
1907	106	163	1962	300	15 789
1908	237	295	1963	178	13 055
1909	176	433	1964	191	6 979
1910	359	825	1965	356	2 654
1911	1 235	2 322	1966	216	2 418
1912	2 319	5 118	1967	89	2 015
1913	2 772	5 594	1968	79	2 385
1914	5 031	4 818	1969	37	2 729
1915	5 536	5 967	1970	20	3 237
1916	4 323	2 881	1971	15	2 149
1917	3 097	1 676	1972	2	1 344
1918	1 978	2 016	1973	1	750
1919	1 994	3 160	1974	0	503
1920	2 948	3 673	1975	0	22
1921	4 443	1 732	1976	0	0
1922	6 689	3 036	1977	0	0
1923	4 657	2 509	1978	0	0
1924	6 510	3 579	1979	0	0
1925	5 787	7 833	1980	0	0
1926	6 976	4 426	1981	0	0
1927	7 827	3 867	1982	0	0
1928	8 954	5 915	1983	0	0
1929	18 267	10 781	1984	0	0
1930	26 637	9 745	1985	0	0
1931	6 613	3 330	1986	0	0
1932	18 308	5 513	1987	0	0
1933	17 307	7 781	1988	0	0
1934	16 569	13 110	1989	0	0
1935	17 672	10 210	1990	0	0
1936	14 420	15 533	1991	0	0
1937	15 022	29 195	1992	0	0
1938	13 092	19 282	1993	0	0
1939	11 010	18 520	1994	0	0
1940	3 245	4 398	1995	0	0
1941	51	1 226	1996	0	0
1942	127	980	1997	0	0
1943	349	1 459	1998	0	0
1944	1 048	1 892	1999	0	0
1945	3 604	9 350	2000	0	0
1946	8 533	14 264	2001	0	0
1947	5 470	20 083	2002	0	0
1948	6 565	17 105			
1949	3 517	17 738			
1950	4 004	15 899			
1951	3 422	18 943			
1952	2 954	19 893			
1953	2 483	24 879			
1954	1 484	24 578	Total	312 221	613 870

Table 4.3: CPUE for fin and blue whale off Durban in terms of numbers caught per number of searching hours per month (Best, P. B. 2003. How low did they go? An historical comparison of indices of abundance for some baleen whales on the Durban whaling ground. IWC Paper SC/55/SH18.

	CPUE (hours/month)	
Year	Fin whale	Blue whale
1920	2.477	1.286
1921		
1922	2.410	1.827
1923	4.427	3.110
1924	3.760	2.244
1925	2.029	2.395
1926	2.469	2.154
1927		2.258
1928	3.534	1.342
1954	7.699	0.152
1955	5.460	0.069
1956	7.216	0.056
1957	8.981	0.060
1958	7.535	0.036
1959	6.403	0.021
1960	7.711	0.056
1961	7.036	0.077
1962	5.054	0.072
1963	3.183	0.041
1964	3.397	0.064
1965	3.963	0.055
1966	1.879	0.039
1967	2.018	
1968	0.974	
1969	2.606	
1970	0.778	
1971	1.278	
1972	0.845	
1973	0.762	
1974	0.436	
1975	0.526	

Table 4.4: Survey abundance estimates in Region A (Areas II+III+IV) and Area III together with the sources of information - see text for further details.

Species	Year	Region	Abundance estimate	Source of information
Fin whale	1997	A	10 591	Mori and Butterworth (2006)
		III	5 426	Branch and Butterworth (2001b)
Blue whale	2000	A	1 104	Mori and Butterworth (2006)
		III	594	Branch and Butterworth (2001b)

Table 4.5: Input values for parameters used in the model (α, β, r_b and r_f), and pre-exploitation abundances (F_o, B_o) together with carrying capacities (K_f, K_b) estimated for Region A and Area III .

Parameters	Region A			Area III		
	Model GR_1		Model GR_2	Model GR_1		Model GR_2
α	0	1.75	1.75	0	1.75	1.75
β	0	0.438	0.625	0	0.438	0.625
R_b	0.063	0.063	0.063	0.063	0.063	0.063
R_f	0.126	0.126	0.126	0.126	0.126	0.126
F_o	307 186	152 579	154 655	134 226	88 853	95 214
B_o	232 678	231 622	229 756	77 740	71 145	72 995
K_f	307 186	557 917	556 728	134 226	222 954	266 715
K_b	232 678	258 323	297 418	77 740	114 651	126 678

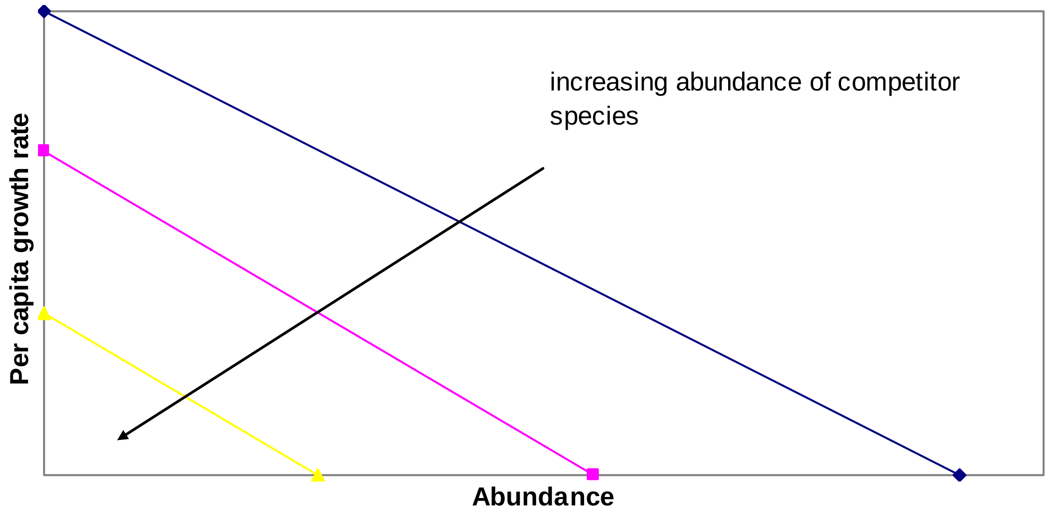


Figure 4.1: Schematic diagram based on Model GR_1 of the effect of an increasing abundance of a competitor species. The primary species cannot maintain its maximum per capita growth rate at low abundance, with this rate dropping as the abundance of the competitor species increases.

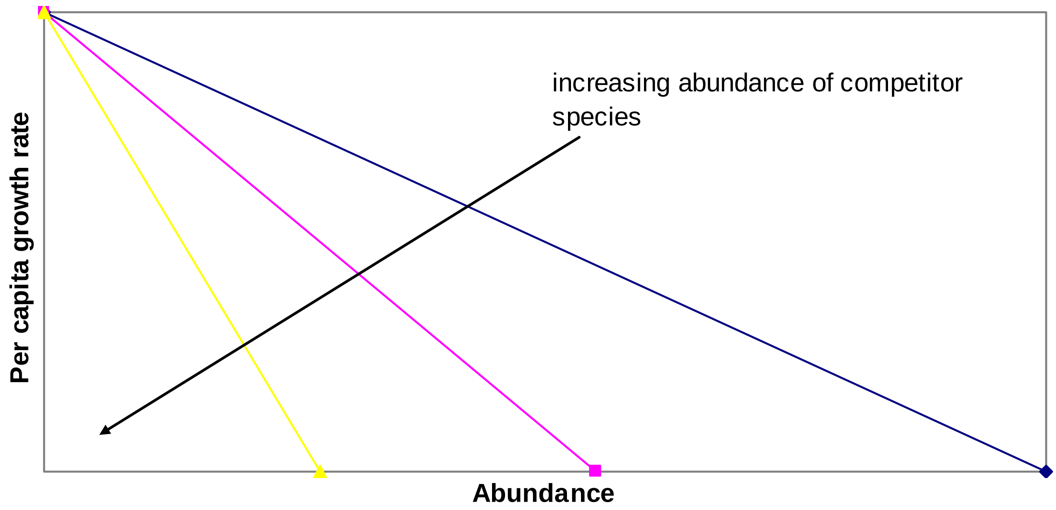


Figure 4.2: Schematic diagram based on Model GR_2 of the effect of an increasing abundance of a competitor species. The primary species maintains its maximum per capita growth rate at low abundance irrespective of the abundance of the competitor species.

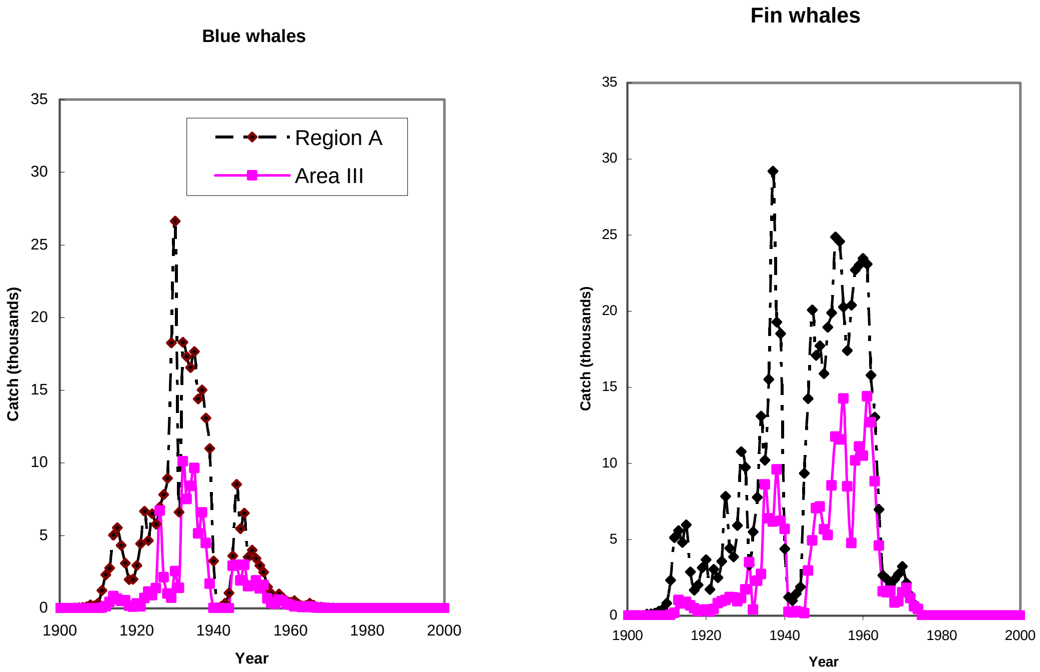


Figure 4.3: Historic annual catches of blue and fin whales in Region A and Area III. Area III data for fin whales were combined across regions south and north of 40°S.

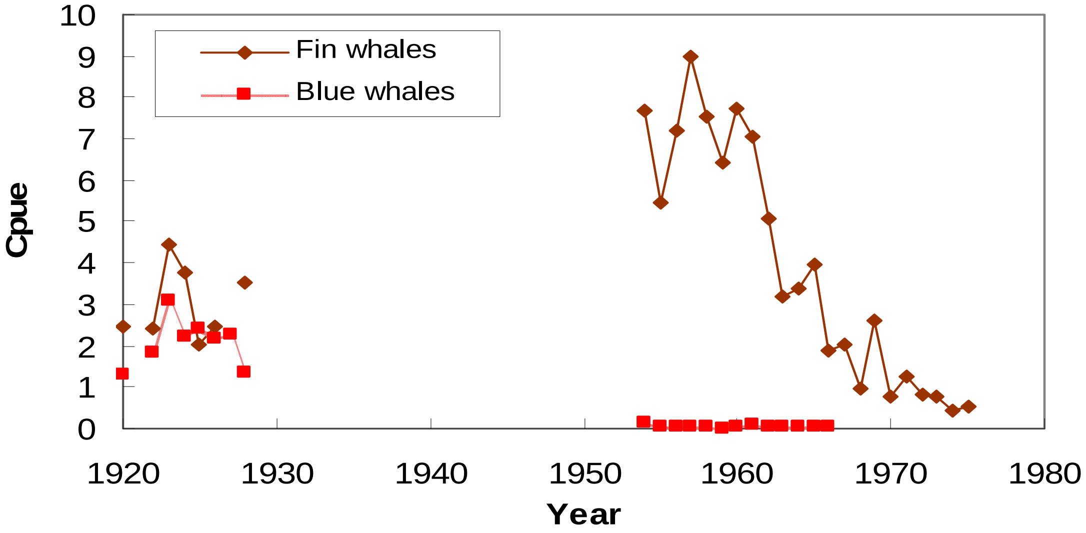


Figure 4.4: CPUE (number of whales caught per hour searching per month) for fin and blue whales of Durban. (Source: P. Best, University of Pretoria [Best, P. B. 2003. How low did they go? An historical comparison of indices of abundance for some baleen whales on the Durban whaling ground. IWC Paper SC/55/SH18.]

Region A

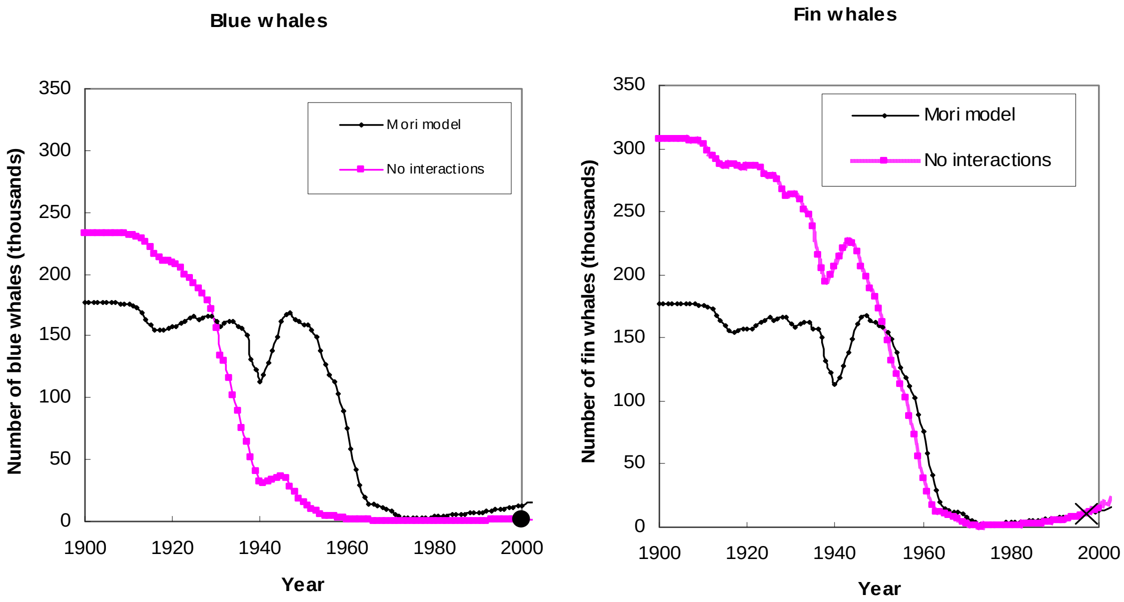
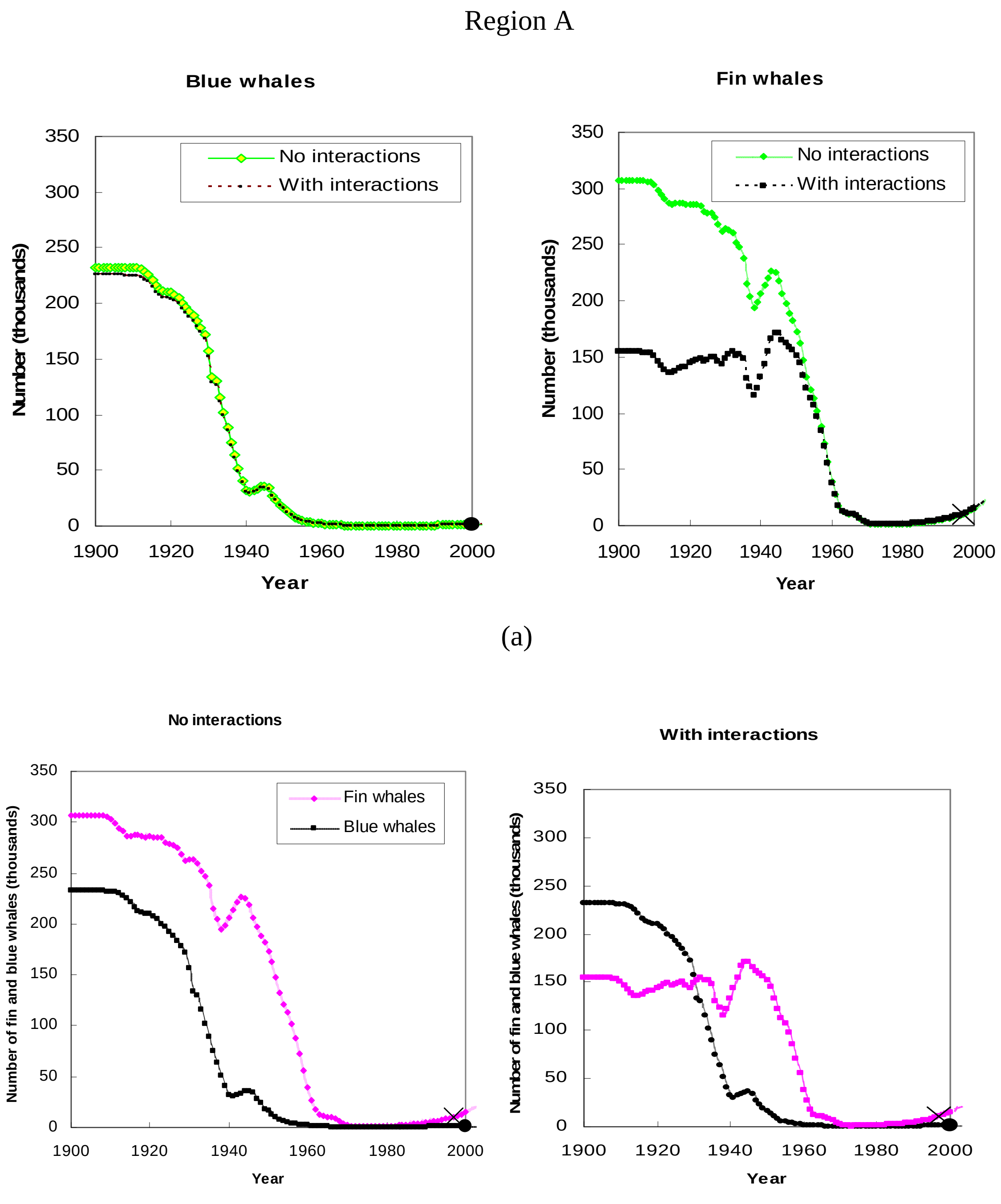


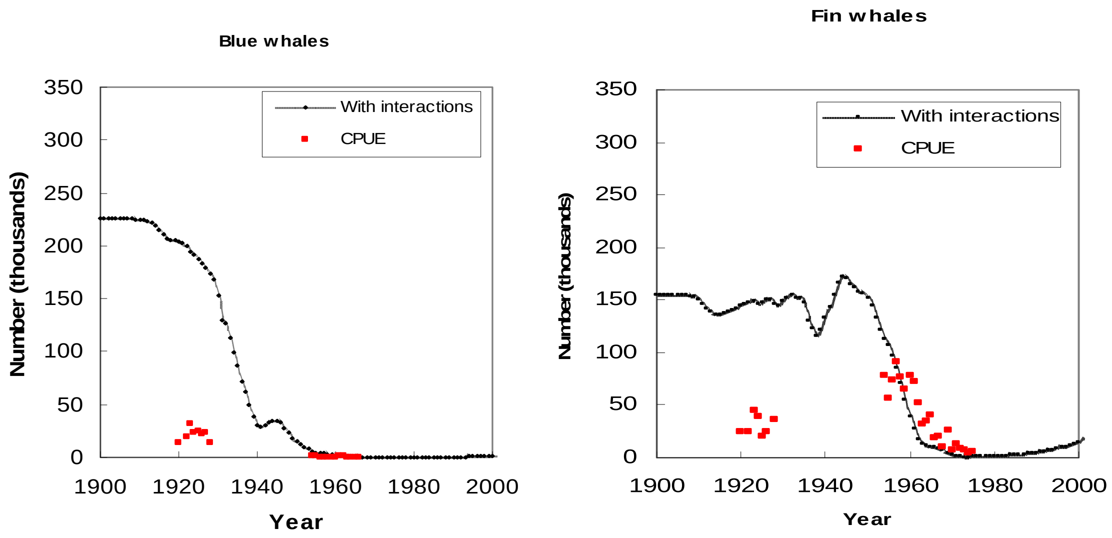
Figure 4.5: Blue and fin whale population trajectories, for Region A based on Model GR_2, but without species interactions; these are compared to the Mori and Butterworth "Reference case" fin whale trajectory which includes inter-species interactions. The cross and black dot are respectively the survey abundance estimates for fin and blue whales through which the model GR_2 trajectories are forced.


Region A

(a)

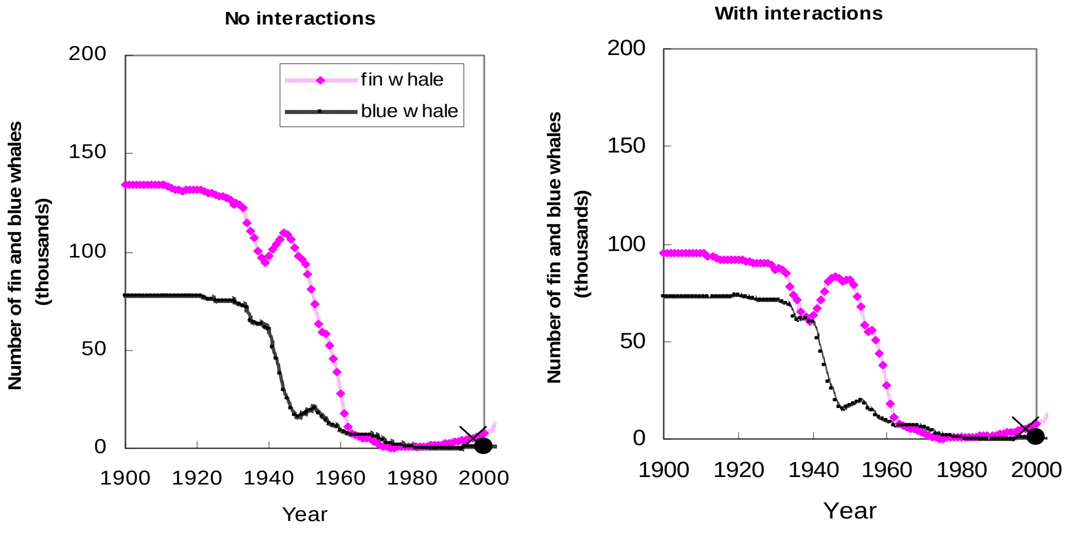
(b)

Figure 4.6: Model GR_2 results for fin and blue whale population trajectories in Region A. The crosses and black dots are respectively the survey abundance estimates for fin and blue whales through which the trajectories are forced. (a) compares results with and without interactions, whereas (b) compares results for blue and fin whales.



Region A

Figure 4.7: Trajectories for blue and fin whales (with competition) in Region A compared to the CPUE data off Durban.



Area III

Figure 4.8: Blue and fin whale population trajectories for Area III. The crosses and black dots are the survey abundance estimates for fin and blue whales respectively through which the trajectories are forced.

Area III

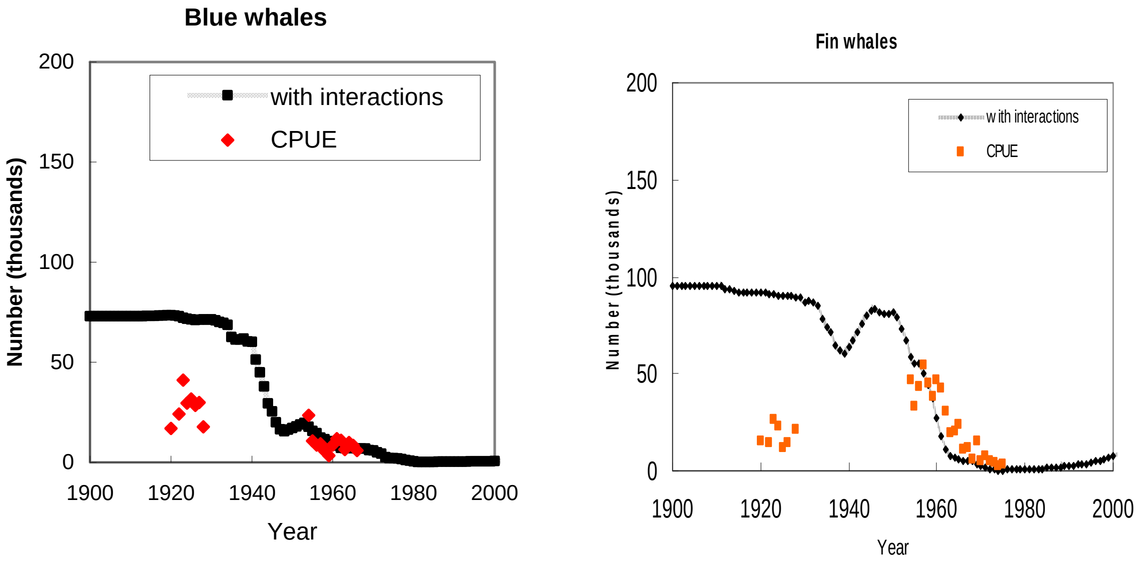


Figure 4.9: Trajectories for blue and fin whales (with competition) in Area III compared to CPUE data off Durban.

Appendix 4.1

Condition for stable mutual co-existence equilibrium

In this Appendix, equations 4.8 and 4.9 are used to determine the stability of the co-existence equilibrium between the two species (the same approach can be used to derive equations 4.5 and 4.6 which indicate similar equilibrium points to equations 4.8 and 4.9 respectively). Population equilibrium occurs in the model when neither of the population levels is changing. In general, competing species can co-exist when interspecific competition is weak. (Nevertheless, even when interspecific competitive interaction is strong, co-existence frequently occurs in a natural community (May and MacArthur 1972).)

Equation 4.8 and 4.9 read:

$$F_{t+1} = F_t + r_f F_t (1 - \frac{F_t}{K_f - \alpha B_t}) - C_t^f$$, and

$$B_{t+1} = B_t + r_b B_t (1 - \frac{B_t}{K_b - \beta F_t}) - C_t^b$$

When F and B are steady the above system of equations yields:

$$F_{t+1} = F_t$$

and

$$B_{t+1} = B_t$$

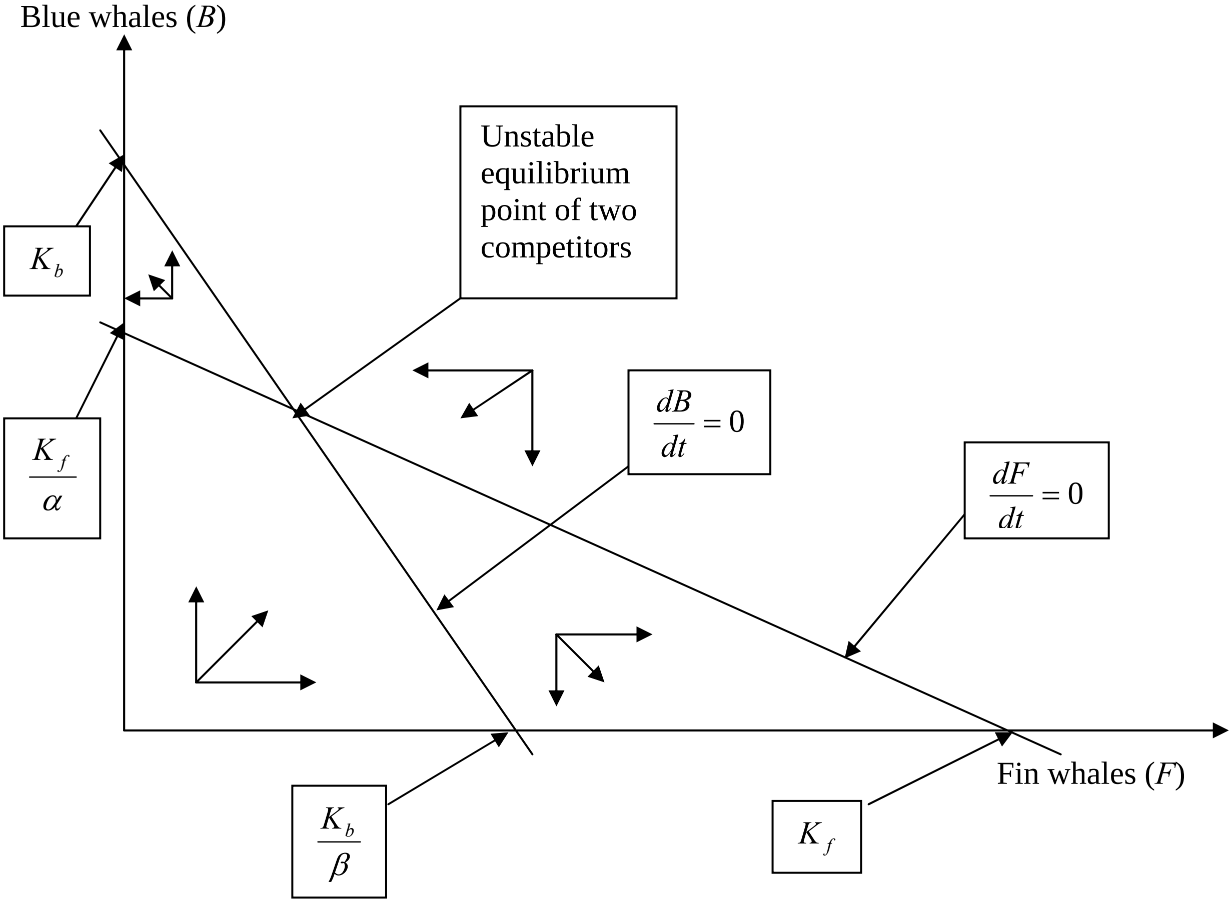
so that for co-existence at t=0

$$\alpha B_o + F_o = K_f$$
$$\beta F_o + B_o = K_b$$

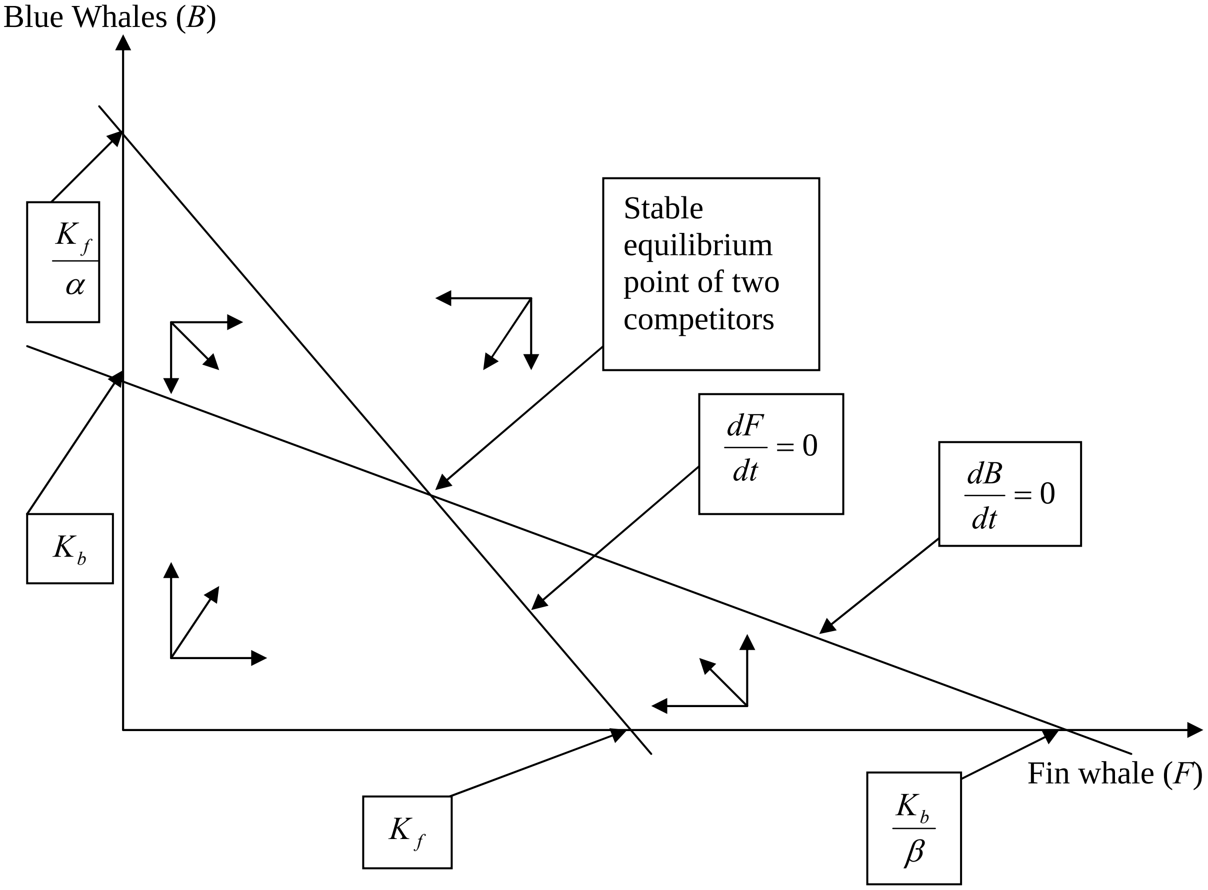
which can be solved for F_o and B_o given α, β, K_f and K_b.

The expected outcome of competition can be examined by considering the phase-plane diagrams for the two species (i.e. plot the zero-growth isoclines) and using vector addition (the arrows) to depict the directions of changes in population size of each species. There are four possible outcomes/cases in the model of competition based on the four ways that the zero-growth isoclines can be arranged.

Case I. Shows example graph of isoclines of zero growth for which one species competitively excludes the other species in order to survive. If $\frac{K_f}{\alpha} < K_b$ and $\frac{K_b}{\beta} < K_f \Rightarrow \alpha\beta > 1 \Rightarrow$ unstable equilibrium point (at the intersection of the isoclines).

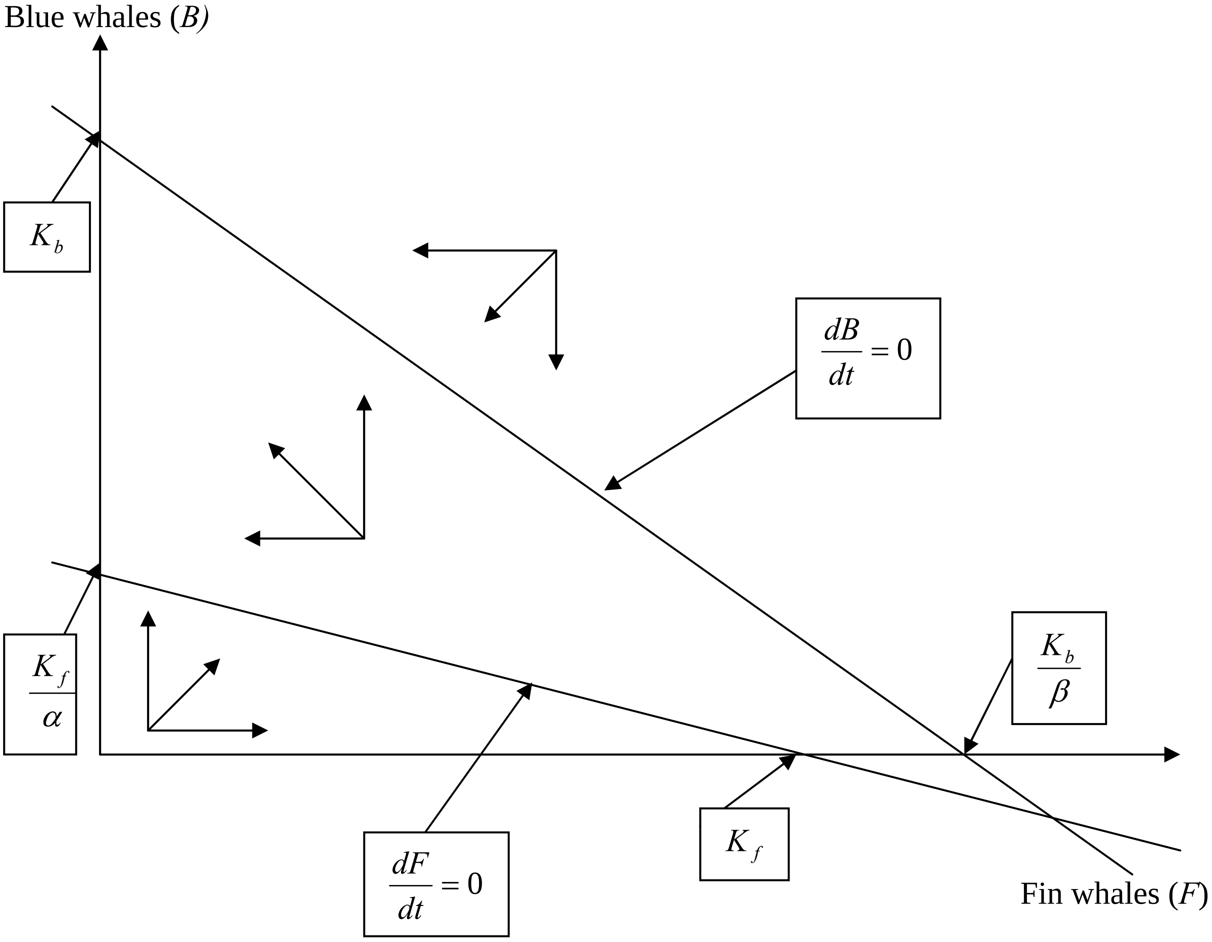


Case II. Shows example graph of isoclines of zero growth for which one species and another species co-exist. If $K_f < \frac{K_b}{\beta}$ and $K_b < \frac{K_f}{\alpha}$ $\Rightarrow \alpha\beta < 1$ $\Rightarrow$ stable equilibrium points (at the intersection of the isoclines)

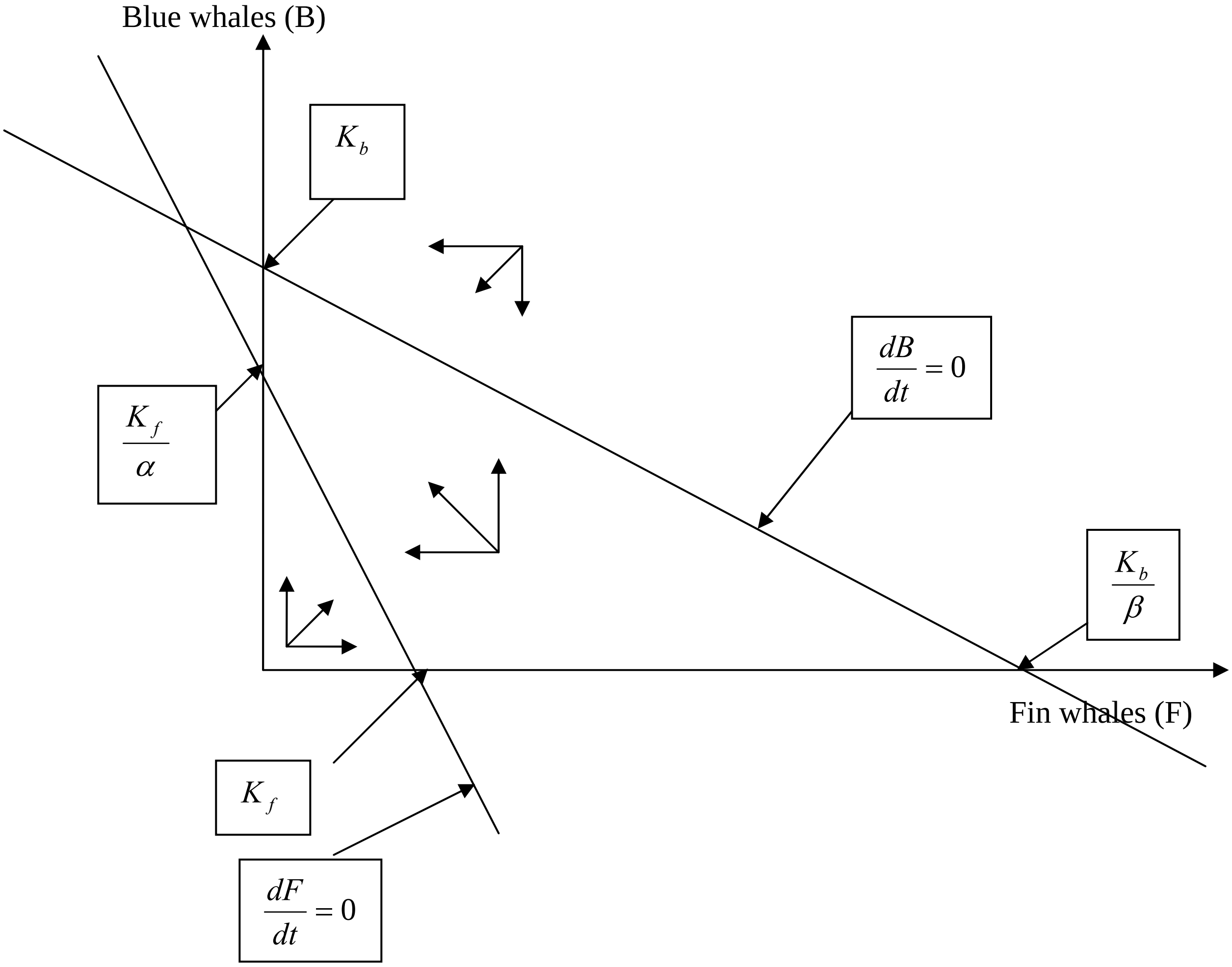


Case III (a) and (b). Show example graphs of isoclines of zero growth for which one species competitively excludes the other species in order to survive. If $\frac{K_f}{\alpha} < K_b$ and $\frac{K_b}{\beta} > K_f$ $\Rightarrow \alpha\beta > 1$ and $\alpha\beta < 1 \Rightarrow$ unstable equilibrium point.

(a) $\alpha\beta > 1$

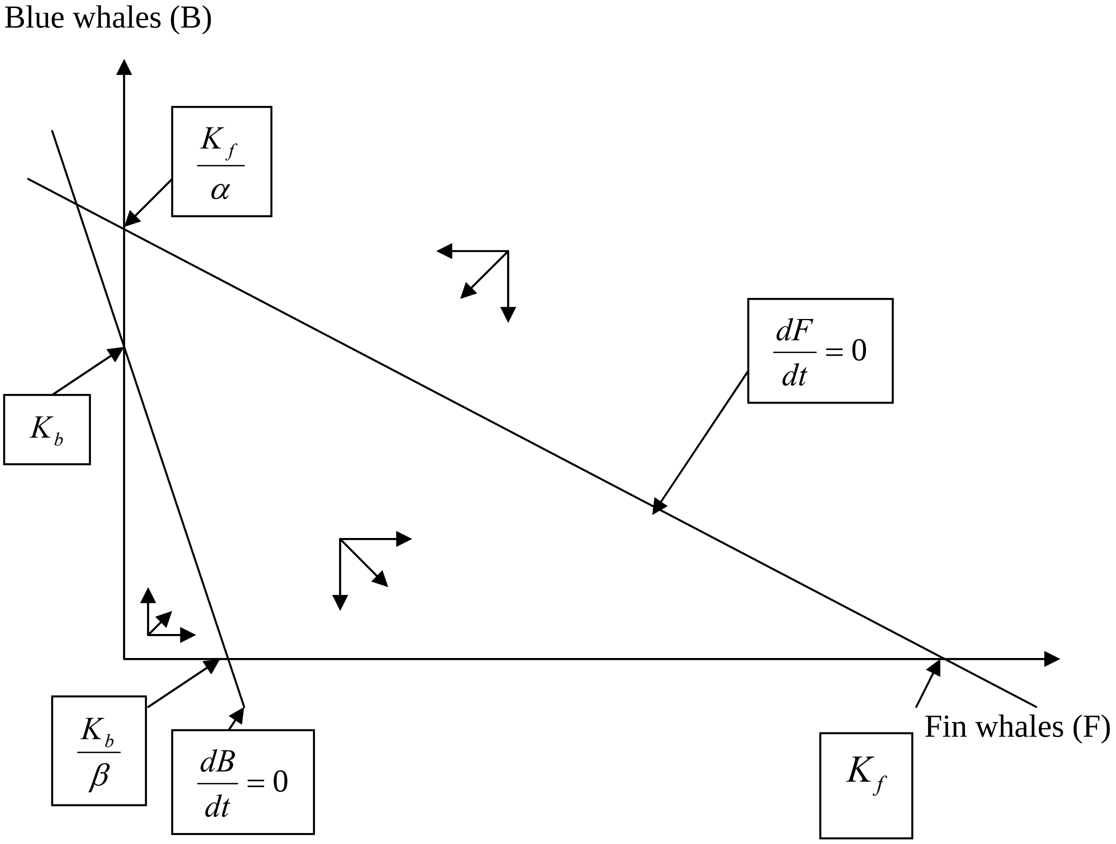


(b) $\alpha\beta < 1$

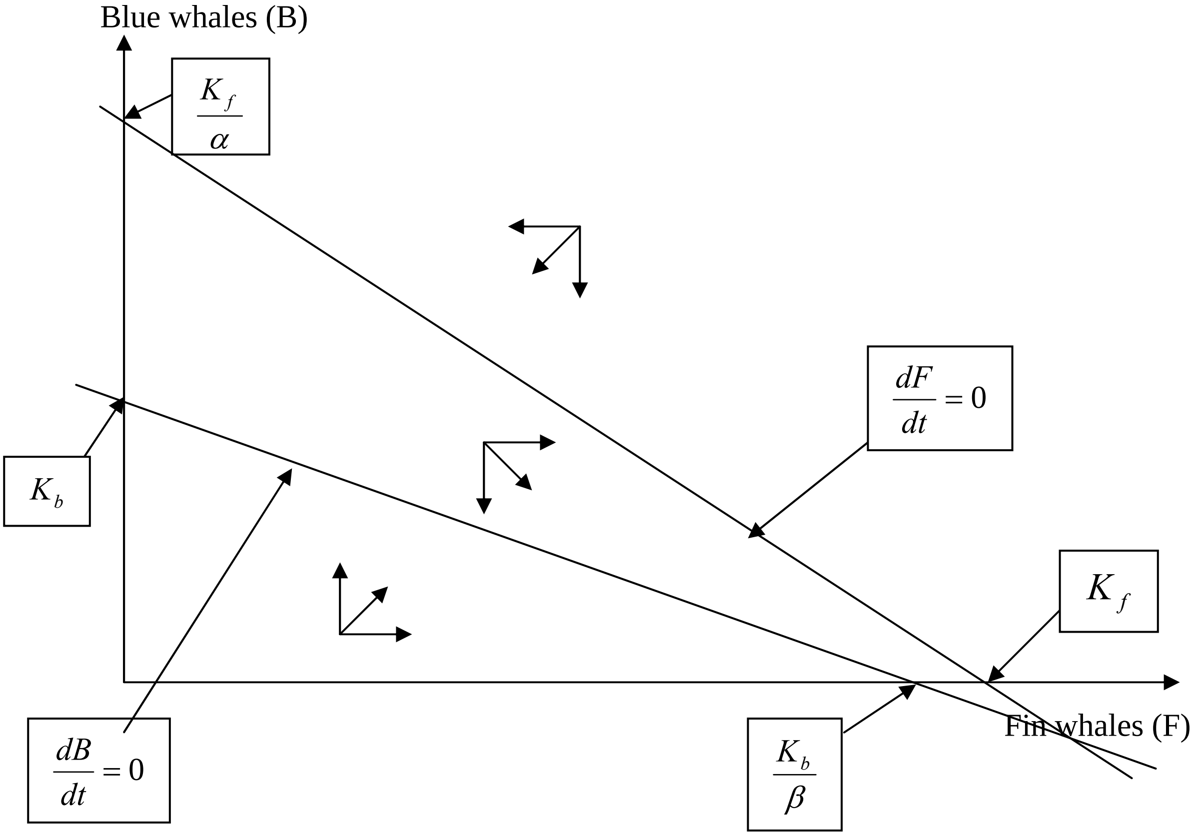


Case IV (a) and (b). Show example graphs of isoclines of zero growth for which one species competitively excludes the other species in order to survive. If $\frac{K_f}{\alpha} > K_b$ and $\frac{K_b}{\beta} < K_f$ $\Rightarrow \alpha\beta > 1$ and $\alpha\beta < 1 \Rightarrow$ unstable equilibrium point.

(a) $\alpha\beta > 1$



(b) $\alpha\beta < 1$



5. EXTENDED MORI AND BUTTERWORTH ANTARCTIC MODEL

5.1 Introduction to the model

This Chapter extends the Mori-Butterworth Antarctic ecosystem model (Chapter 2) to include squid as a species with fast dynamics compared to whales and seals. The form of the species interaction reflected by equations (2.1) and (2.2) is well known in predator-prey models. These models are frequently used in ecology and have been extensively analyzed (e.g. Holling, 1965; Cushing and Saleen, 1982; Kindlmann and Dixon, 2001). All predator-prey models rely heavily on parameters estimated from feeding studies. Most of the dietary of mysticetes (baleen whales) are well known. For example it is well known that most mysticetes eat small schooling fishes and variety of crustaceans such as krill, copepods and amphipods.

The reduction of seals (in the 18th – 19th centuries) and whales (20th century) through harvesting caused the increase of krill biomass. Mori and Butterworth (2006) model the inter-species competition of seals and whales to check which species were the first to benefit from krill biomass after competitive release. They concluded that minke whales and crabeater seals were the first to benefit from krill biomass. However the model considered only species with slow dynamics. The reasons why squid is included in the model is to see if it can predict fast dynamics species to be the ones that took advantage of krill surplus before minke whales and crabeater seals as suggested by Mori and Butterworth (2006). Squid is chosen as a representative of other fast dynamic species.

5.2 Material and methods

5.2.1 Available data for species considered in the model

The catch data for fin, minke and humpback whales considered in the model were obtained from C. Allison (IWC Secretariat). Rademeyer *et al.* (2003) provides data for blue whales. Humpback whales caught in Region A relate to catches for breeding stocks A, B, C and D while those in Region P relate to catches for breeding stocks E, F and G. This study considered only Region A because the numbers of baleen whales harvested in the southern Atlantic/Indian Oceans were far greater than elsewhere in the Southern Hemisphere. The catches of the four species considered are listed in Table 4.2 and Table 5.1. Catches for seals are given in Table 5.2. More details on how the fur seal catch series was developed are given in Appendix 5.1.

Table 5.3 shows the input values adopted by Mori and Butterworth (2006) for the parameters considered in the model and also the reference case value assumed for squid (see section 5.3). Values which are used to calculate the rate of consumption of krill for each species λ^j for Region A together with the sources for this information are given in Table 5.4, while Table 5.5 shows the values of λ^j that result together with the values assumed for other demographic parameters. Absolute abundance estimates for the species considered in the model for Region A are shown in Table 5.6. Note that there are no data on squid abundance available for use when fitting the model. Table 5.7 shows abundance trends for the predator species considered in the model. Note that abundance trends for fin whales and crabeater seals are not well known and hence these species are not included in this table.

The biological parameter values in these Tables are as assumed by Mori and Butterworth (2006) for the species which they considered. For squid, a typical mass of 1 *kg* was assumed with a high consumption rate of 10% of body weight per day (Table 5.4). In Table 5.5, M^{sq} was set to 2, this being typical of the rates listed in section 3.4, with μ^{sq} set at 4 to ensure a high possible population growth rate given the value for M^{sq}.

5.2.2 Description and parameterization of the model

This subsection describes the addition of a predator with fast dynamics, such as squid, to the Mori and Butterworth model. Eight species are thus included in the model described here. The model is used to estimate their population trends in terms of numbers or biomass. Such models need information concerning the functional relationship between predator growth rates and prey availability. Since this information is scarce, the present study assumed Holling Type III response curves to apply (Holling, 1965).

The biomass of krill in region *a* is calculated as:

$$B^a_{y+1} = B^a_y + r^a B^a_y \left(1 - \frac{B^a_y}{K_a}\right) - \sum_j \frac{\lambda^j \left(B^a_y\right)^2 N^{j,a}_y}{\left(B^{j,a}\right)^2 + \left(B^a_y\right)^2} - \frac{\lambda^{sq} \left(B^a_y\right)^2 N^{sq,a}_y}{\left(B^{sq,a}\right)^2 + \left(B^a_y\right)^2} \tag{5.1}$$

and the number of squid in region *a* in year *y* is calculated as:

$$N^{sq,a}_{y+1} = N^{sq,a}_y + \frac{\mu^{sq} N^{sq,a}_y \left(B^a_y\right)^2}{\left(B^{sq,a}\right)^2 + \left(B^a_y\right)^2} - M^{sq} N^{sq,a}_y - \eta^{sq,a} (N^{sq,a}_y)^2 \tag{5.2}$$

where

j = blue whale, minke whale, humpback whale, fin whale, crabeater seals or Antarctic fur seals;

μ^{sq} is the maximum annual per capita recruitment rate of squid;

$N_y^{sq,a}$ is the number of squid in region *a* in year *y*;

$B^{sq,a}$ is the krill biomass when the consumption rate and hence also the per capita recruitment rate for squid in region *a* drops to half of its maximum level;

M^{sq} is the natural annual mortality rate of squid; and

$\eta^{sq,a}$ is a parameter governing the density dependence of natural mortality and/or birth rate for squid in region *a*.

Assuming a steady state for the year 1780 and setting $B_{y+1}^a = B_y^a$ and $N_{y+1}^{sq,a} = N_y^{sq,a}$ equations 5.1 and 5.2 lead respectively to the following equations:

$$r^a B_{1780}^a \left(1 - \frac{B_{1780}^a}{K_a}\right) = \sum_j \frac{\lambda^j \left(B_{1780}^a\right)^2 N_{1780}^{j,a}}{\left(B^{j,a}\right)^2 + \left(B_{1780}^a\right)^2} + \frac{\lambda^{sq} \left(B_{1780}^a\right)^2 N_{1780}^{sq,a}}{\left(B^{sq,a}\right)^2 + \left(B_{1780}^a\right)^2} \tag{5.1}$$

and

$$\frac{\mu^{sq} N_{1780}^{sq,a} \left(B_{1780}^a\right)^2}{\left(B^{sq,a}\right)^2 + \left(B_{1780}^a\right)^2} = M^{sq} N_{1780}^{sq,a} + \eta^{sq,a} (N_{1780}^{sq,a})^2 \tag{5.2}$$

In order to calculate the krill biomass associated with squid when at half its maximum per capita recruitment level, the initial biomass of krill B_{1780}^a must be specified first. This can be calculated from equation 5.2 using any species considered in the model. To be consistent with Mori and Butterworth (2006), the blue whale equation was used, which results in the following formula:

$$B_{1780}^a = \frac{B^{b,a} \sqrt{M^b + \eta^{b,a} N_{1780}^{b,a}}}{\sqrt{\mu^b - M^b - \eta^{b,a} N_{1780}^{b,a}}} \tag{5.3}$$

When B_{1780}^a is known, then the krill biomass at which the consumption rate for squid and hence also the squid per capita recruitment rate in region *a* drop to half of their maximum levels is calculated as:

$$B^{sq,a} = \sqrt{\frac{\left(B_{1780}^{a}\right)^2\left(\mu^{sq} - M^{sq} - \eta^{sq,a}N_{1780}^{sq,a}\right)}{M^{sq} + \eta^{sq,a}N_{1780}^{sq,a}}} \tag{5.4}$$

Once B_{1780}^{a} and $B^{sq,a}$ are known, the carrying capacity of krill in the absence of predators in region *a* (K_a) can be calculated as follows using equation 5.1:

$$K_a = \frac{r^a B_{1780}^{a}}{r^a - \sum_j \frac{\lambda^j B_{1780}^{a} N_{1780}^{j,a}}{\left(B^{j,a}\right)^2 + \left(B_{1780}^{a}\right)^2} - \frac{\lambda^{sq} B_{1780}^{a} N_{1780}^{sq,a}}{\left(B^{sq,a}\right)^2 + \left(B_{1780}^{a}\right)^2}} \tag{5.5}$$

The annual consumption rate of krill by a predator of type *j* is calculated by Mori and Butterworth (2006) as follows:

λ^j = (mean weight)^j × (%weight consumption/day)^j × (days feeding in the Antarctic)^j × (estimated proportion of krill in diet)^j (5.6)

The same basis is used to calculate the consumption rate of krill by squid λ^{sq}. Assumed values for the mean weight, %weight consumption/day, days feeding in the Antarctic and the estimated proportion of krill in diet for squid are listed in Table 5.4. Other parameter values that are used for whales, seals and krill, including $B^{b,a}$, M^j, η^j, r^a and μ^j, are the same or very similar to those used by Mori and Butterworth (2006). The choice of high values for the squid recruitment and natural mortality rate parameters (i.e. μ^{sq} and M^{sq}) follows from the literature review (see Chapter 3).

After specifying the model, the next step is the maximization of the likelihood function to estimate the values of the remaining parameters based upon the data available. This process is described in the following subsection.

5.2.3 The likelihood function

A likelihood function provides the relative probability of the data given a particular set of parameter values (Hilborn and Mangel, 1997). The conceptual motivation behind parameter estimation is to pick that value of the parameter which has the highest probability of giving rise to the data observed. Usually the negative log-likelihood (- *ln L*) function is minimized to estimate such "best" values for parameters. More details of the negative log-likelihood function used in this study are given in the Appendix 5.2.

As no data are available for squid to use in fitting the model (so that terms such as LL^{sq}_{abun} and/or LL^{sq}_{tren} can not be included in the equation for the negative log-likelihood equation in Appendix 5.2), parameters for squid cannot be estimated in this process. Thus instead different values are fixed at input, and then the parameters for the other species are estimated conditional on these values for squid by maximising the likelihood using AD Model Builder™.

5.3 RESULTS AND DISCUSSION

The model is used to produce trajectories of each species under several different scenarios corresponding to different choices for parameter values. First a "Reference case" model is considered in which the parameters for species (other than squid) are kept at the values assumed by Mori and Butterworth (2006).

Reference case

To initiate computations including squid, a Reference case was specified with the squid parameters N^{sq}_{1780} and η^{sq} set to 8×10^{6} and 4×10^{-9} respectively. "Reference case" biomass trajectories for squid, crabeater seals and minke whales together with estimated parameter values for all species are shown in Figure 5.2a and Table 5.8 respectively. The reason for focusing on minke whales and crabeater seals are that these are the first species that benefit from the "krill surplus" in terms of the Mori and Butterworth (2006) model, so that it is important to see whether such trends also hold when squid is added to the model.

The trajectories indicate that squid abundance in the model started to increase from about 1920 until about the 1940s (Figure 5.2a). By about 1950 squid biomass had reached a maximum and started to decrease slowly until about 1990, and then more rapidly. By comparison minke whales and crabeater seals started to increase from about 1930, and then to drop after reaching maxima in about 1980. Evidently, because of its faster dynamics, squid benefitted first from the krill surplus as heavy whale harvests commenced around 1920, but by 1940 the squid growth rate was reduced to zero by density dependence and increasing krill consumption by minke whales and crabeater seals.

Figure 5.3 shows the "Reference case" trajectories of all species considered in the model. The abundance of each predator depends on the abundance of the other predators because of competition for krill as a shared prey resource (equation 2.1). Over the period 1780 – 1840, seals decreased in response to hunting and therefore the model predicts a slight increase in whale numbers over this period. The model simulation projects the population of each species under an assumption of zero catch from the year 2000. The trajectories suggest that blue whales, humpback whales and fin whales will increase in the future until they reach their pre-exploitation abundances; due to these increases krill biomass will decrease and this will lead to a decrease in the squid population (Figure 5.4).

This study indicates that results were particularly sensitive to the values of the parameter governing the density dependence of natural mortality and/or birth rate, η; hence it is important to explore this further.

Sensitivity tests

The impact of the following model changes were examined in sensitivity tests:

i. Increase squid abundance.
ii. Decrease the density dependence of natural mortality and/or birth rate for squid.
iii. Remove squid from the model and vary parameters for density dependence of natural mortality and/or birth rate for minke whales and crabeater seals.
iv. Fix the pre-exploitation abundance of squid and vary the parameters governing the density dependence of natural mortality and/or birth rate for crabeater seals, minke whales and squid.

Results of the scenarios investigated are presented as follows: Table 5.9 shows different values of the input values for squid together with estimated biomasses in the year 2000 and maximum biomasses for squid, minke whale and crabeater seals for scenarios (i) and (ii). Tables 5.10 and 5.11 are developed in a similar manner for scenarios (iii) and (iv) respectively.

For scenarios (i) and (ii), when compared to the Reference case results, the feature of a sharp increase in squid from about 1920 does not change. Results hardly change when the initial abundance of squid is increased (scenario (i)) - see Table 5.9 and Figure 5.2(b). However, when the η parameter for squid is decreased (scenario (ii)), the squid biomass reaches larger levels. While minke whales and crabeater seals biomasses reach about the same maximum, the start of their increases is delayed compared to the Reference case (Tables

5.9a,b and Figure 5.2c). This shows that the squid biomass trajectory is relatively insensitive to initial squid abundance but depends strongly on the value of the η^{sq} parameter.

For scenario (iii), when squid is not considered in the model, a decrease in the density dependent mortality rate parameter for minke whales results in an increase in the maximum biomass of minke whales, while the maximum for crabeater seals decreases slightly compared to the Reference case (Table 5.10a and Figure 5.5b (1)). When the density dependent mortality rate parameter for crabeater seals is decreased, the biomass of crabeater seals, which peaks in the 1970s, generally increases while results for minke whales do not change qualitatively (Table 5.10b; also compare Figure 5.5 for the "Reference case' and Figure 5.5b (2)).

Table 5.10c shows biomasses estimated for minke whales and crabeater seals when the η parameter for minke whales is fixed and reduced compared to the Reference case, and the η parameter varied for crabeater seals. This shows that both minke whales and crabeater seals reach higher maximum biomasses than in the Reference case.

The following results are evident when examining scenario (iv).

1. When the value of η^{c} is decreased from its Reference case value of 7×10^{-9} together with fixed η^{m} and η^{sq} parameters, the maximum biomass of crabeater seals is variable, whereas the minke whale maximum biomass shows an increase and that for squid remains unchanged. The fit to the data does however deteriorate when compared to the $-\ln L$ of the Reference case, suggesting that these smaller η^{c} parameter values are not consistent with the data (see Table 5.11a and Figure 5.6b (1)).
2. When the value of η^{m} is decreased from its Reference case value of 3×10^{-7}, with fixed η^{c} and η^{sq} parameters, the start of the increase in minke whales is delayed compared to the Reference case. Trajectory trends for minke whales do not show a similar pattern to the Reference case, peaking a few years later around 1990 compared to around the 1980 for the Reference case, while trajectories for crabeater seals and squid scarcely change from the Reference case (Figure 5.6b (2)). Maximum biomass for squid hardly differs as η^{c} and η^{m} are changed (Tables 5.11a-b); similarly, the maximum biomass for crabeater seals hardly changes as η^{m} is changed (Table 5.11b). However, fits to the data are worse as η^{m} decreases.

3. When the value of η^{sq} is decreased while η^{c} and η^{m} remain fixed (Table 5.11c), the biomass trends for minke whales and crabeater seals show a similar pattern to the Reference case, peaking around the 1970s (compare Figure 5.6 for the Reference case and Figure 5.6b (3)). Under this scenario, the declining trend from the 1980s for squid is greatly reduced compared to the Reference case. The fits to the data are worse for smaller η^{sq}.

In summary, a sensitivity analysis for scenario (iv) revealed that when the values of the η^{m}, η^{c}, and η^{sq} are decreased from their Reference case value, some differences in biomass trends result, but the model fit to the data always deteriorates.

Overview of the impact of squid on model results

Key features of the model-predicted results are:

- Squid started to increase at about the same time (1920) that the reduction of large baleen whales (blue, humpback and fin whales) commenced under heavy harvesting. This suggests that species with fast dynamics such as squid may have been the first to benefit from the krill surplus, whereas minke whales and crabeater seals started to increase only about a decade later.

- Squid biomass started to drop rapidly in the late 1980s because of a predicted decrease in krill biomass decreased during the 1970s to 1980s, and because of density dependent mortality effects.

- The inclusion of squid in the model hardly impacts the maxima reached by other species in the model benefiting from the krill surplus (when compared to the Mori and Butterworth results), though when squid biomass is great, the increases in abundance of minke whales and crabeater seals are delayed.

Overall, although the results show that the inclusion of a species with fast dynamics has qualitatively little impact on the model results, the model predicts that squid were probably the first species to benefit from the krill surplus (rather than minke whales and crabeater seals as suggested by Mori and Butterworth (2006)).

Difficulties with the model

There are three important difficulties with this model when squid is included as an example of a species with fast dynamics.

1) There is no information on abundance or its trend for squid. Thus there are not any data for squid which can be used when fitting the model, and alternative fixed values need to be used as inputs.
2) Knowledge of the biological parameters of squid is limited so these have to be fixed at values which are not reliably determined. This adds to the uncertainties associated with the results.
3) There is little information upon which to base the η parameters specifying density dependence, to which results are very sensitive.

5.4 CONCLUSIONS

The use of a biomass–based model such as the Mori-Butterworth Antarctic ecosystem model to assess the impacts of fast dynamic species (such as squid) on slow dynamic species (such as whales and seals) was necessitated by the available data, which do not include the age-structure of the catches. The extended Mori-Butterworth Antarctic ecosystem model presented in this Chapter allows for the evaluation of the interaction between fast and slow dynamic species. Although this model is a useful starting point to understand trophic interactions, its design focuses only on high trophic level interactions. The results from this Chapter illustrate the usefulness of a more comprehensive approach to the design of the Mori-Butterworth model. The results suggest that it is important to consider the interaction between fast and slow dynamic species, rather than considering only species with slow dynamics.

This approach could serve as a foundation for an assessment of a squid fishery. For example, results from the model presented here could be fed into an integrated assessment that incorporates not only squid, whales and seals in the model, but also other species such as icefish and Patagonian toothfish.

Table 5.1: Historical catches in the Atlantic/Indian (Region A) of baleen whales considered in this study (see text for details on sources). Note that catches for fin and blue whales in Region A are given in Table 4.2.

Year	Minke	Humpback	Year	Minke	Humpback
	Region A	Region A		Region A	Region A
1900	0	0	1955	36	1 270
1901	0	0	1956	45	1 946
1902	0	0	1957	10	3 700
1903	0	180	1958	9	4 279
1904	0	288	1959	3	3 250
1905	0	240	1960	2	1 069
1906	0	1 261	1961	2	1 826
1907	0	2 170	1962	8	515
1908	0	3 936	1963	114	91
1909	0	6 578	1964	58	1 150
1910	0	8 566	1965	74	427
1911	0	8 818	1966	381	580
1912	0	9 856	1967	1 113	0
1913	0	6 256	1968	606	0
1914	0	3 254	1969	752	0
1915	0	915	1970	914	0
1916	0	73	1971	4 157	3
1917	0	95	1972	6 583	1
1918	0	211	1973	7 271	0
1919	0	283	1974	5 280	0
1920	0	229	1975	5 350	0
1921	1	1 503	1976	6 117	0
1922	0	1 386	1977	4 126	0
1923	0	1 000	1978	4 954	0
1924	0	1 957	1979	5 609	0
1925	0	1 345	1980	4 697	0
1926	0	1 128	1981	4 845	0
1927	0	1 198	1982	3 935	0
1928	0	227	1983	4 136	0
1929	0	1 159	1984	3 504	0
1930	0	255	1985	3 470	0
1931	0	464	1986	2 935	0
1932	0	1 030	1987	273	0
1933	0	3 219	1988	0	0
1934	0	5 874	1989	327	0
1935	0	12 562	1990	0	0
1936	0	13 637	1991	288	0
1937	0	4 596	1992	0	0
1938	0	2 447	1993	330	0
1939	0	455	1994	0	0
1940	0	92	1995	439	0
1941	0	0	1996	0	0
1942	0	84	1997	438	0
1943	0	175	1998	0	0
1944	0	284	1999	439	0
1945	0	123	2000	0	0
1946	0	134			
1947	0	289			
1948	0	5 693			
1949	1	4 858			
1950	0	3 299			
1951	4	2 039			
1952	6	1 794			
1953	12	1 540			
1954	0	2 401			
			Total	83 654	151 563

Table 5.2: Catch series for Antarctic fur seals (Region A only) developed by Mori and Butterworth (2006); including assumed annual harvests of 750 crabeater seals in Region A from 1967 to 1977.

Year	Antarctic fur seals	Year	Crabeater seal
1790	0	1965	0
1791	1 100	1966	0
1792	2 200	1967	750
1793	3 300	1968	750
1794	4 400	1969	750
1795	5 500	1970	750
1796	6 600	1971	750
1797	7 700	1972	750
1798	8 800	1973	750
1799	9 900	1974	750
1800	11 000	1975	750
1801	104 500	1976	750
1802	99 000	1977	750
1803	93 500	1978	0
1804	9 900	1979	0
1805	93 500	1980	0
1806	8 800	1981	0
1807	82 500	1982	0
1808	7 700	1983	0
1809	71 500	1984	0
1810	66 000	1985	0
1811	60 500	1986	0
1812	55 000	1987	0
1813	49 500	1988	0
1814	44 000	1989	0
1815	38 500	1990	0
1816	22 000	1991	0
1817	16 500	1992	0
1818	11 000	1993	0
1819	5 500	1994	0
1820	0	1995	0
1821	32 0000	1996	0
1822	284 444	1997	0
1823	248 888	1998	0
1824	213 332	1999	0
1825	177 776	2000	0
1826	142 220		
1827	106 664		
1828	71 108		
1829	35 552		
1830	0		
Total	3 249 984	Total	8 250

Table 5.3: Input values for the parameter η^j (year^{-1}) governing the density dependence of natural mortality and/or birth (and calf survival) rate (for predator species considered in the model), the intrinsic growth rate of krill in Regions A as assumed by Mori and Butterworth (2006) and the Reference case value assumed for squid.

Parameters	Input values for Region A
η^b	4.00×10^{-8}
η^m	3.00×10^{-7}
η^f	4.00×10^{-8}
η^h	1.25×10^{-6}
η^s	3.50×10^{-9}
η^c	7.00×10^{-9}
η^{sq}	4.00×10^{-8}
r	0.400
B^b	1.70×10^8 tons

Table 5.4: Values which are used to calculate the annual rate of consumption of krill for each species considered in the model (λ^j). Data are taken from Mori and Butterworth (2006) for all species except squid, which is discussed in the text.

Species	Mean weight (t)	%weight consumption/day in Region A	Days feeding in the Antarctic	Estimated proportion of krill in diet (%)
Blue whale	103	3.5	125	100
Minke whale	6	5.1	90	100
Humpback whale	27	4	100	100
Fin whale	46	4	120	100
Antarctic fur seal	0.2	7	323	60
Crabeater seal	0.2	7	335	94
Squid	0.001	10	365	100

Table 5.5: Input values for the annual consumption rate of krill, birth rate and natural mortality rate of predators considered in the model. The basis for the choice of the values of the parameters λ^{sq}, μ^{sq} and M^{sq} is described in the text (λ^{j} (tons/year), μ^{j} (year^{-1}), M^{j} (year^{-1})). The other values are as used by Mori and Butterworth (2006).

Parameters	Input values
λ^{b}	451
λ^{m}	32.1
λ^{f}	110.4
λ^{h}	108
λ^{s}	2.71
λ^{c}	5.51
λ^{sq}	0.04
μ^{b}	0.160
μ^{m}	0.200
μ^{f}	0.16
μ^{h}	0.18
μ^{s}	0.280
μ^{c}	0.236
μ^{sq}	4
M^{b}	0.030
M^{m}	0.044
M^{f}	0.049
M^{h}	0.080
M^{s}	0.070
M^{c}	0.074
M^{sq}	2

Table 5.6: Absolute abundance estimates for the species considered in the model for Region A. Note that there are no data on squid abundance available for use when fitting the model.

Species	Year	Abundance estimate in Region A	CV	Source of information
Blue whale	2000	1104	0.4	Rademeyer *et al.* (2003)
Fin whale	1997	10591	0.5	Branch and Butterworth (2001b), Butterworth and Geromont (1995)
Humpback whale	1997	5044	0.2	Branch and Butterworth (2001b)
Minke whale	1985	327369	0.1	IWC (1991)
Antarctic fur seals	1930	100	0.5	Payne (1977, 1979)
	1975	369000	0.5	Payne (1977, 1979), MacCann and Doidge (1987)
Crabeater seals	1990	1550000	0.5	Boyd (1993)
	2000	4000000	0.5	Mori and Butterworth (2006) (cited from J. Laake)
Squid	-	-	-	-

Table 5.7: Abundance trends for predators considered in the model. Note that abundance trends for fin whales and crabeater seals are not well known and hence are not included in this table. For blue whales the trend is estimated when fitting the model to the abundance estimates available for the three years listed.

Species	Year	Fitted trends	CV	Source
Blue whale	1981	546	0.41	Branch and Rademeyer (2003)
	1988	680	0.52	
	1996	1891	0.42	
Humpback whale	1977-1991	0.11	0.14	Bannister (1994)[1]
	1981-1996	0.12	0.07	Brown *et al*. (1997)[2]
Minke whale	1970-2000	-0.024	0.31	Mori and Butterworth (2005)[3]
	1970-2000	-0.024	0.31	
Antarctic fur seals	1957-1972	0.17	0.5	Payne (1977, 1979)
	1976-1990	0.10	0.5	Payne (1977), Boyd *et al*. (1995)
	1990-1999	0.10	0.5	Boyd (1993), SSG (2000)
Squid	-	-	-	See Table 5.6 caption

[1] For west Australia (Area IV) only.

[2] For east Australia (Area V) only.

[3] For Areas IV and V only.

Table 5.8: A comparison of estimates of predator trajectory values for the Mori and Butterworth (2006) model, and for the "Reference case" model in this thesis which includes squid, which fixes $\eta^{sq} = 4\times10^{-9}$, $\eta^{m} = 3\times10^{-7}$ and $\eta^{c} = 7\times10^{-9}$. Part (a) shows estimable parameters reflecting pre-exploitation equilibrium abundances in the initial year 1780 and –ln*L*, whereas (b) shows abundance and trend estimates for recent years for which observations are available.

(a)

	Bounds	M&B (N^{sq} =0)	Reference case
$N_{1780}^{b,A}$	(100000,300000)	162332	180325
$N_{1780}^{m,A}$	(10000,200000)	47155	6859
$N_{1780}^{h,A}$	(10000,250000)	71589	72191
$N_{1780}^{f,A}$	(10000,400000)	151505	175533
$N_{1780}^{s,A}$	(500000,5000000)	2898590	2925440
$N_{1780}^{c,A}$	(10000,10000000)	241045	268356
N_{1780}^{sq}			8×10^{6}(fixed)
-ln L		2.38	5.56

(b)

	Observed	M&B (N^{sq} =0)	Reference case
$N_{2000}^{b,A}$	1104	1109	1114
$N_{1985}^{m,A}$	327369	325963	346148
$N_{1997}^{h,A}$	5044	5046	5040
$N_{1997}^{f,A}$	10591	10649	10777
$N_{1930}^{s,A}$	100	175	171
$N_{1975}^{s,A}$	369000	262422	180064
$N_{1990}^{s,A}$	1550000	1234240	1410550
$N_{2000}^{c,A}$	4000000	241045	11362400
$R_{1970-2000}^{m,A}$	-0.024	-0.017	-0.013
$R_{1977-1991}^{h,A}$	0.11	0.09	0.10
$R_{1958-1971}^{s,A}$	0.17	0.19	0.20
$R_{1977-1991}^{s,A}$	0.10	0.17	0.19
$R_{1991-2000}^{s,A}$	0.10	0.10	0.14

Table 5.9: Maximum and current biomass of squid, minke whales and crabeater seals in relation to alternative assumed input values for the pre-exploitation abundance of squid (N_{1780}^{sq}) and the squid density dependent mortality rate parameter (η^{sq}) for scenarios (i) and (ii). The reference case is shown in bold.

(a)

N_{1780}^{sq}	η^{sq}	2000 biomass (million tons)			Max biomass (million tons)		
		Squid	Minke	Crabeater	Squid	Minke	Crabeater
8×10^{6}	**4×10^{-9}**	**0.3**	**1.3**	**2.2**	**0.5**	**2.1**	**3.8**
8×10^{6}	3×10^{-9}	0.3	1.9	3.0	0.7	2.4	3.7
12×10^{6}	3×10^{-9}	0.4	1.9	3.1	0.7	2.4	4.0
20×10^{6}	3×10^{-9}	0.3	1.8	3.0	0.7	2.2	4.0

(b)

N_{1780}^{sq}	η^{sq}	2000 biomass (million tons)			Max biomass (million tons)		
		Squid	Minke	Crabeater	Squid	Minke	Crabeater
8×10^{6}	1.8×10^{-9}	0.4	1.1	1.8	1.1	2.5	3.9
12×10^{6}	1.8×10^{-9}	0.5	1.9	3.1	1.1	2.4	4.0
20×10^{6}	1.8×10^{-9}	0.9	2.5	3.9	1.1	2.5	4.1

(c)

N_{1780}^{sq}	η^{sq}	2000 biomass (million tons)			Max biomass (million tons)		
		Squid	Minke	Crabeater	Squid	Minke	Crabeater
8×10^{6}	1×10^{-9}	1.9	1.1	1.9	2	2.5	4.0
12×10^{6}	1×10^{-9}	0.5	1.8	3.0	2	2.5	4.1
20×10^{6}	1×10^{-9}	0.9	1.2	1.8	2	2.5	3.7

Table 5.10: Table of results for minke whale and crabeater seals when squid was excluded from the model (scenario iii). Part (a) shows results when η^{m} is varied for fixed η^{c} and (b) and (c) shows similar results when η^{m} is fixed and η^{c} allowed to vary. The results for the Mori and Butterworth (2006) model are shown in bold.

(a)

η^{m}	η^{c}	-ln*L*	2000 biomass (million tons)		Max biomass (million tons)	
			Minke	Crabeater	Minke	Crabeater
3×10^{-7}	**7×10^{-9}**	**3.3**	**1.7**	**2.5**	**2.7**	**3.2**
1×10^{-7}	7×10^{-9}	178	4.2	2.3	4.4	2.8
3×10^{-8}	7×10^{-9}	73	2.6	0.8	4.5	2.5
1×10^{-8}	7×10^{-9}	75	2.3	0.9	2.7	2.7
3×10^{-9}	7×10^{-9}	3.3	4.3	2.3	6.4	2.7
1×10^{-9}	7×10^{-9}	117	3.6	1.4	3.6	3.0

(b)

η^{m}	η^{c}	-ln*L*	2000 biomass (million tons)		Max biomass (million tons)	
			Minke	Crabeater	Minke	Crabeater
3×10^{-7}	**7×10^{-9}**	**3.3**	**1.7**	**2.5**	**2.7**	**3.2**
3×10^{-7}	5×10^{-9}	31	1.4	2.8	2.7	5.6
3×10^{-7}	1×10^{-9}	145	0.5	3.4	2.5	5.5
3×10^{-7}	0.5×10^{-9}	25	1.4	2.8	2.5	3.8
3×10^{-7}	0.1×10^{-9}	172	0.4	3.9	2.5	6.3

(c)

η^{m}	η^{c}	-ln*L*	2000 biomass (million tons)		Max biomass (million tons)	
			Minke	Crabeater	Minke	Crabeater
3×10^{-9}	5×10^{-9}	70	2.5	1.1	2.7	3.8
3×10^{-9}	1×10^{-9}	75	3.5	3.0	4.1	5.2
3×10^{-9}	0.5×10^{-9}	53	2.8	3.5	3.8	5.7
3×10^{-9}	0.1×10^{-9}	48	1.7	3.5	2.9	6.3

Table 5.11: Table of results for scenario (iv) for squid, minke whale and crabeater seals when the pre-exploitation abundance of squid (N^{sq}_{1780}) is fixed. Part (a) shows results as η^c is varied for a fixed η^m and η^{sq}; (b) shows results as η^m is varied for a fixed η^{sq} and η^c; and (c) shows results as η^{sq} is varied for a fixed η^c and η^m. The Reference case is shown in bold.

(a)

N^{sq}_{1780}	η^{sq}	η^m	η^c	-ln*L*	2000 biomass (million tons)			Max biomass (million tons)		
					Squid	Minke	Crabeater	Squid	Minke	Crabeater
8×10^{6}	**4×10^{-9}**	**3×10^{-7}**	**7×10^{-9}**	**3.3**	**0.3**	**1.3**	**2.2**	**0.5**	**2.1**	**3.8**
8×10^{6}	4×10^{-9}	3×10^{-7}	5×10^{-9}	55.14	0.2	2.0	3.7	0.5	2.4	4.1
8×10^{6}	4×10^{-9}	3×10^{-7}	1×10^{-9}	153.07	0.5	2.9	2.8	0.5	2.9	2.8
8×10^{6}	4×10^{-9}	3×10^{-7}	0.5×10^{-9}	161.95	0.5	3.1	3.5	0.5	3.1	3.5
8×10^{6}	4×10^{-9}	3×10^{-7}	0.1×10^{-9}	162.47	0.5	3.1	3.4	0.5	3.1	3.4

(b)

N^{sq}_{1780}	η^{sq}	η^m	η^c	-ln*L*	2000 biomass (million tons)			Max biomass (million tons)		
					Squid	Minke	Crabeater	Squid	Minke	Crabeater
8×10^{6}	**4×10^{-9}**	**3×10^{-7}**	**7×10^{-9}**	**3.3**	**0.3**	**1.3**	**2.2**	**0.5**	**2.1**	**3.8**
8×10^{6}	4×10^{-9}	1×10^{-7}	7×10^{-9}	43.43	0.2	2.5	2.2	0.5	2.7	3.9
8×10^{6}	4×10^{-9}	3×10^{-8}	7×10^{-9}	43.88	1.8	3.6	2.2	0.5	3.6	3.9
8×10^{6}	4×10^{-9}	3×10^{-9}	7×10^{-9}	44.89	0.2	5.4	2.4	0.5	5.4	3.7
8×10^{6}	4×10^{-9}	1×10^{-9}	7×10^{-9}	136.07	0.2	4.6	2.2	0.5	4.6	3.9

(c)

N^{sq}_{1780}	η^{sq}	η^m	η^c	-ln*L*	2000 biomass (million tons)			Max biomass (million tons)		
					Squid	Minke	Crabeater	Squid	Minke	Crabeater
8×10^{6}	**4×10^{-9}**	**3×10^{-7}**	**7×10^{-9}**	**3.3**	**0.3**	**1.3**	**2.2**	**0.5**	**2.1**	**3.8**
8×10^{6}	3×10^{-9}	3×10^{-7}	7×10^{-9}	11.78	0.2	0.9	1.8	1.1	2.3	3.8
8×10^{6}	1.8×10^{-9}	3×10^{-7}	7×10^{-9}	458.93	0.4	1.1	1.8	1.1	2.5	3.9
8×10^{6}	1×10^{-9}	3×10^{-7}	7×10^{-9}	387.88	2.0	2.9	3.9	2.0	2.9	3.9

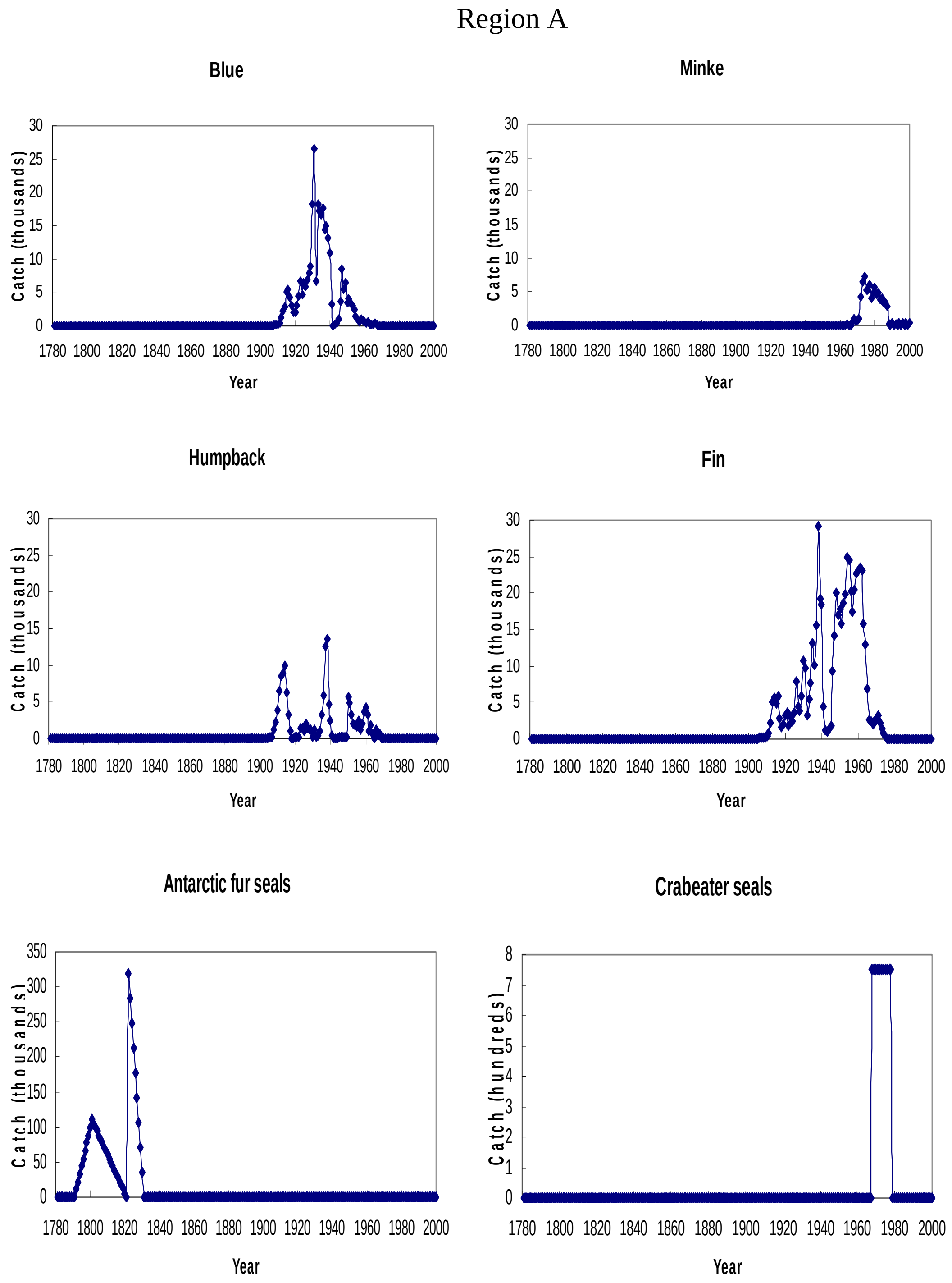
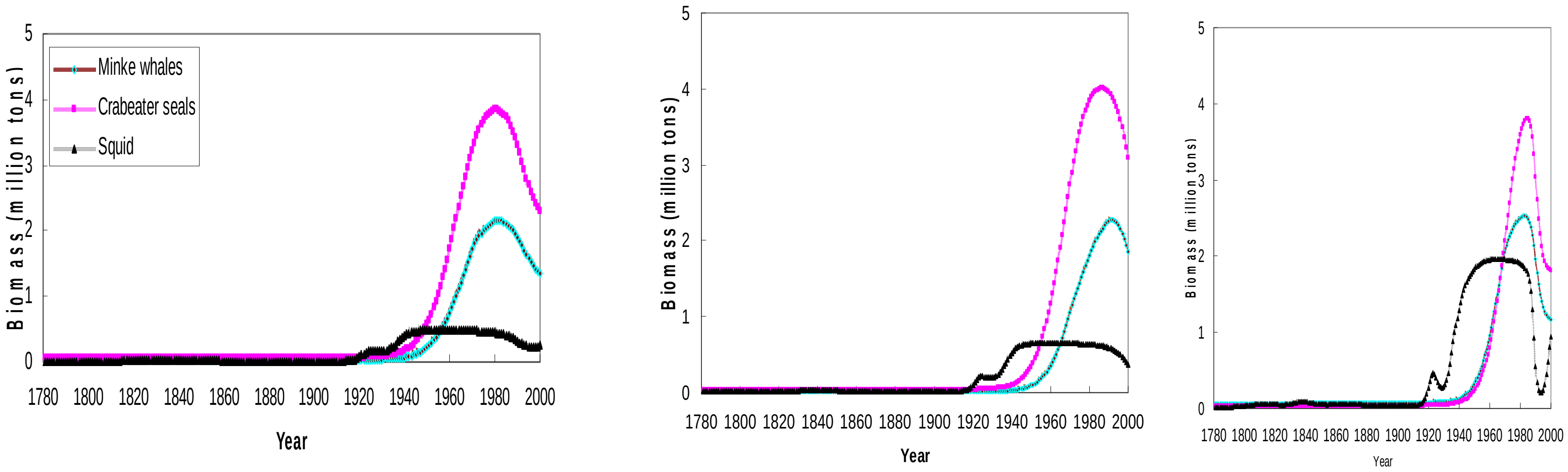


Figure 5.1: Historical catches of species considered in the model for Region A (IWC Management Areas II, III and IV).



(a) Reference case

(b) Scenario (i)

(c) Scenario (ii)

Figure 5.2: Trajectories for minke whales, crabeater seals and squid: (a) Reference case, (b) represents results for scenario (i) where initial abundance of squid in the Reference case is increased from 8×10^{6} to 20×10^{6} and (c) shows results for scenario (ii) where the parameter governing the density dependence of natural mortality rate for squid η^{sq} in the Reference case decreases from 4×10^{-9} to 1×10^{-9}.

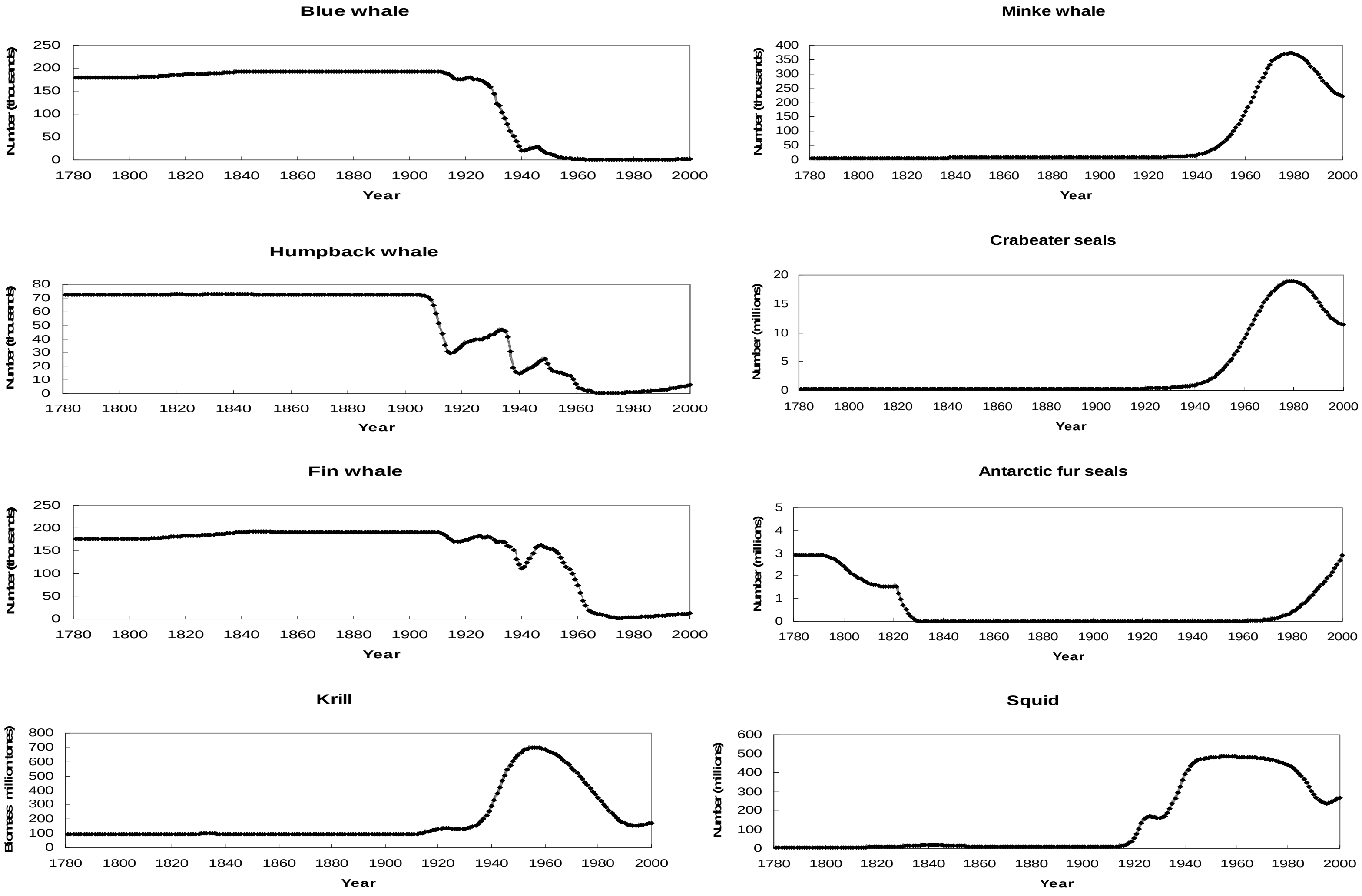


Fig 5.3: "Reference case" trajectories for all species considered in the model for Region A.

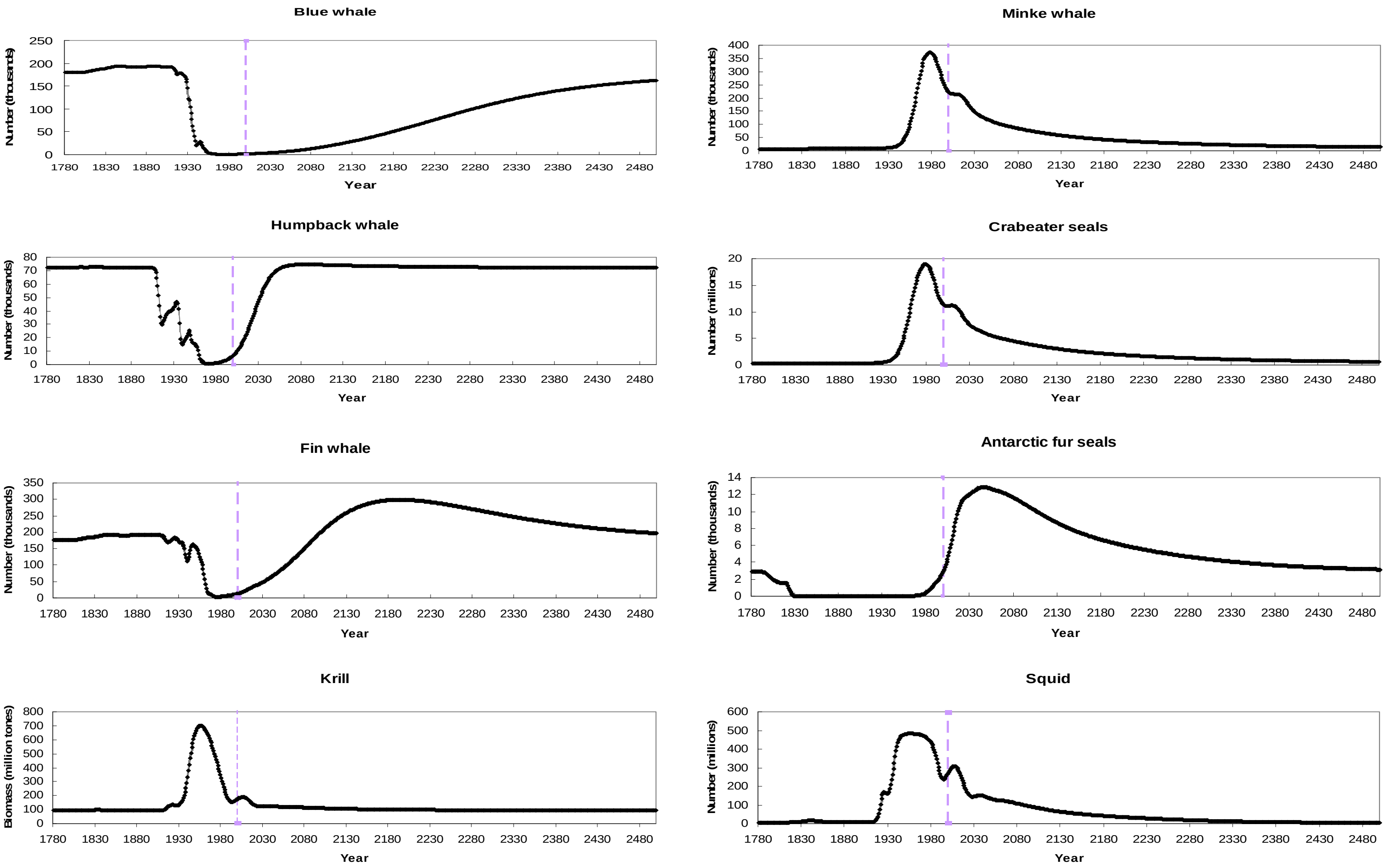


Figure 5.4: "Reference case" trajectories for each species considered in the model shows future population under zero catch after 2000 (indicated by doted lines).

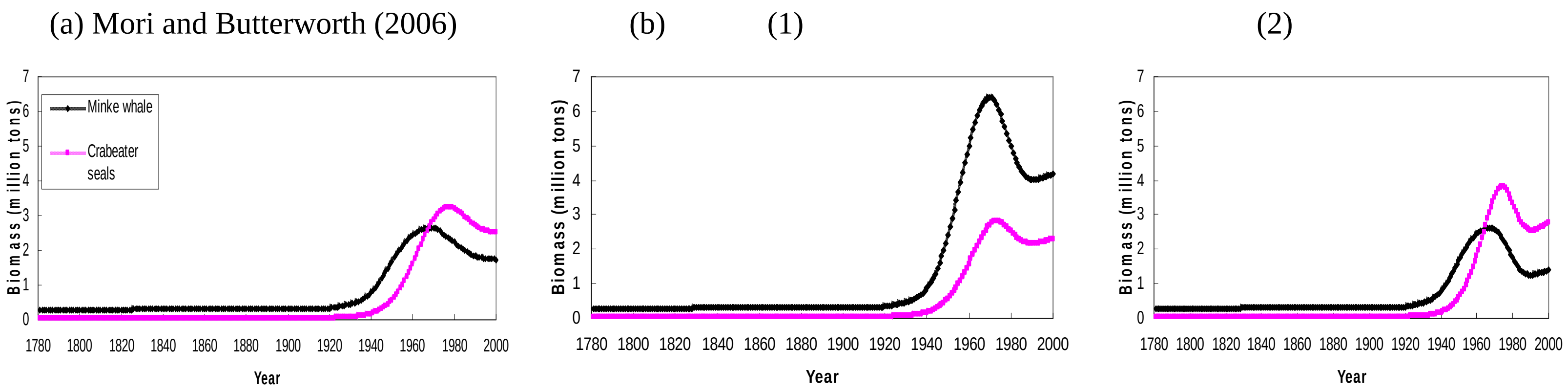
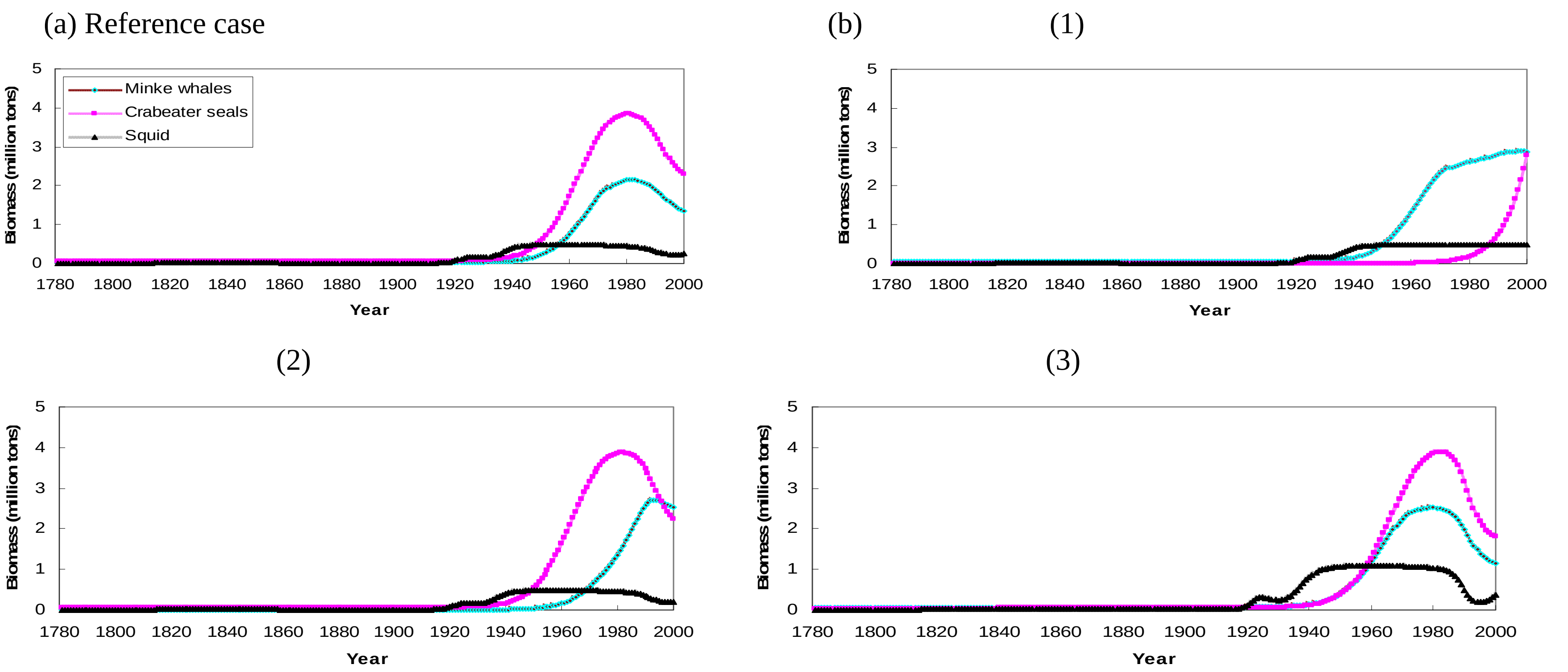


Figure 5.5: Trajectories for minke whales and crabeater seals for scenario (iii) where squid are not considered in the model,: (a) Mori and Butterworth (2006) (baseline case); (b) results when (1) the crabeater seal density dependence parameter is fixed at 7×10^{-9} while the corresponding minke whale parameter is decreased by two order of magnitude from the value for baseline case, and (2) the minke whale density dependence parameter is fixed at 3×10^{-7} while the corresponding crabeater seal parameter is decreased to 0.5×10^{-9} from the value for the baseline case.


(a) Reference case

(b) (1)

(2)

(3)

Figure 5.6: Trajectories for minke whales, crabeater seals and squid for scenario (iv) where pre-exploitation abundance of squid is fixed ($N^{sq}_{1780} = 8\times10^{6}$): (a) Reference case; (b) (1) minke whale and squid density dependence parameters are fixed at their baseline values while the corresponding crabeater seal parameter is decreased to 1×10^{-9} from its baseline value; (b) (2) crabeater seal and squid density dependence parameters are fixed at their baseline values while the corresponding minke whale parameter is decreased to 1×10^{-7} from its baseline value; and (b) (3) crabeater seal and minke whale density dependence parameters are fixed at their baseline values while the corresponding squid parameter is decreased to 3×10^{-9} from its baseline value.

Appendix 5.1

Functions used to calculate catches of Antarctic fur seals

For South Georgia these functions are:

C_y = 11000 - (y-1790)   for $1790 \le y \le 1800$

C_y = 110000 – 5500(y-1790)   for $1801 \le y \le 1820$

where C_y is the catch of Antarctic fur seals for South Georgia for year y. For the South Shetland Islands the function is:

C_y = 320000 – 35556(y-1790)   for $1821 \le y \le 1829$

The information used to develop these equations is described in Mori and Butterworth (2006).

Appendix 5.2

Likelihood Function

The negative log-likelihood function minimized in fitting the model is as used by Mori and Butterworth (2006):

$$-\ln L = LL^{b}_{abun} + LL^{b}_{tren} + LL^{m}_{abun} + LL^{m}_{tren} + LL^{h}_{abun} + LL^{h}_{tren} + LL^{f}_{abun} + LL^{s}_{abun} + LL^{s}_{tren} + LL^{c}_{abun}$$

where

- LL^{j}_{abun} is the component that compares the model estimated abundance of predator species j to the observed abundance (estimated directly from surveys) and assumes distribution lognormality;
- LL^{j}_{tren} is the component pertinent to the abundance trend which is assumed to be normally distributed about its expected value.

The LL^{j}_{abun} and LL^{j}_{tren} component for each species j are given by:

Blue whales

$$LL^{b}_{abun} = \frac{\left(\ln N^{b,A}_{2000} - \ln \hat{N}^{b,A}_{2000}\right)^2}{2\left(\sigma^{b,A}_{2000}\right)^2} + \frac{\left(\ln N^{b,P}_{2000} - \ln \hat{N}^{b,P}_{2000}\right)^2}{2\left(\sigma^{b,P}_{2000}\right)^2}$$

$$LL^{b}_{tren} = \sum_{y=1}^{n}\left[\ln\sigma_y + \frac{1}{2\sigma_y^2}\left(\ln N_y^{b,obs} - \ln q - \ln\hat{N}_y^{b}\right)^2\right]$$

Minke whales

$$LL^{m}_{abun} = \frac{\left(\ln N_{1985}^{m,A} - \ln\hat{N}_{1985}^{m,A}\right)^2}{2\left(\sigma_{1985}^{m,A}\right)^2} + \frac{\left(\ln N_{1985}^{m,P} - \ln\hat{N}_{1985}^{m,P}\right)^2}{2\left(\sigma_{1985}^{m,P}\right)^2}$$

$$LL^{m}_{tren} = \frac{\left(R_{1970-2000}^{m,A} - \hat{R}_{1970-2000}^{m,A}\right)^2}{2\left(\sigma_{1970-2000}^{m,A}\right)^2} + \frac{\left(R_{1970-2000}^{m,P} - \hat{R}_{1970-2000}^{m,P}\right)^2}{2\left(\sigma_{1970-2000}^{m,P}\right)^2}$$

Humpback whales

$$LL^{h}_{abun} = \frac{\left(\ln N_{1997}^{h,A} - \ln\hat{N}_{1997}^{h,A}\right)^2}{2\left(\sigma_{1997}^{h,A}\right)^2} + \frac{\left(\ln N_{1997}^{h,P} - \ln N_{1997}^{h,P}\right)^2}{2\left(\sigma_{1997}^{h,P}\right)^2}$$

$$LL^{h}_{tren} = \frac{\left(R_{1977-1991}^{h,A} - \hat{R}_{1977-1991}^{h,A}\right)^2}{2\left(\sigma_{1977-1997}\right)^2} + \frac{\left(R_{1981-1996}^{h,P} - \hat{R}_{1981-1996}^{h,P}\right)^2}{2\left(\sigma_{1981-1996}^{h,P}\right)^2}$$

Fin whales

$$LL^{f}_{abun} = \frac{\left(\ln N_{1997}^{f,A} - \ln\hat{N}_{1997}^{f,A}\right)^2}{2\left(\sigma_{1997}^{f,A}\right)^2} + \frac{\left(\ln N_{1997}^{f,P} - \ln\hat{N}_{1997}^{f,P}\right)^2}{2\left(\sigma_{1997}^{f,P}\right)^2}$$

Antarctic fur seals

$$LL^{s}_{abun} = \frac{\left(\ln N_{1930}^{s,A} - \ln\hat{N}_{1930}^{s,A}\right)^2}{2\left(\sigma_{1930}^{s,A}\right)^2} + \frac{\left(\ln N_{1976}^{s,A} - \ln\hat{N}_{1976}^{s,A}\right)^2}{2\left(\sigma_{1976}^{s,A}\right)^2} + \frac{\left(\ln N_{1991}^{s,A} - \ln\hat{N}_{1991}^{s,A}\right)^2}{2\left(\sigma_{1991}^{s,A}\right)^2}$$

$$LL^{s}_{tren} = \frac{\left(R_{1958-1971}^{s,A} - \hat{R}_{1958-1971}^{s,A}\right)^2}{2\left(\sigma_{1958-1971}^{s,A}\right)^2} + \frac{\left(R_{1977-1991}^{s,A} - \hat{R}_{1977-1991}^{s,A}\right)^2}{2\left(\sigma_{1977-1991}^{s,A}\right)^2} + \frac{\left(R_{1991-2000}^{s,A} - \hat{R}_{1991-2000}^{s,A}\right)^2}{2\left(\sigma_{1991-2000}^{s,A}\right)^2}$$

Crabeater seals

$$LL^{c}_{abun} = \frac{\left(\ln N_{2000}^{c,A} - \ln\hat{N}_{2000}^{c,A}\right)^2}{2\left(\sigma_{2000}^{c,A}\right)^2} + \frac{\left(\ln N_{2000}^{c,P} - \ln\hat{N}_{2000}^{c,P}\right)^2}{2\left(\sigma_{2000}^{c,P}\right)^2}$$

where

- $\sigma_y^{j,a}$ is the CV of the observed abundance (or abundance trend) of species j in a region a in year(s) y;

- $R_{y_1-y_2}^{j,a}$ is the rate of increase of species j in region a from year y_1 to year y_2 which is calculated from the equation $R_{y_1-y_2}^{j,a} = \left(\frac{N_{y_2}^{j,a}}{N_{y_1}^{j,a}}\right)^{\frac{1}{y_2-y_1}} - 1$;

- ln$q$ is used to indicate a possible multiplicative bias in the abundance estimates utilized and is given by: $\ln q = \frac{\sum_{y=1}^{n} \frac{1}{\sigma_y^2}\left(\ln N_y^{b,obs} - \ln \hat{N}_y^b\right)}{\sum_{y=1}^{n} \frac{1}{\sigma_y^2}}$.

6. SYNTHESIS AND FUTURE RESEARCH

In the last two centuries, the Southern Hemisphere region has seen substantial commercial harvesting first of seals and then whales. This harvesting of whales and seals may indirectly impact non-target species of seals and whales as well as fishes and birds through predator-prey interactions. This study addressed two topics.

1. The assessment of the initial of fin whale population size before exploitation based on a simple model for fin whales and their interaction with other species (see Chapter 4).
2. The assessment of the impact of introducing a further predator with fast dynamics, such as squid, into the Mori-Butterworth Antarctic ecosystem model (see Chapter 5).

The interest for addressing the first topic arises because the Mori-Butterworth Antarctic ecosystem model yielded a surprising result for fin whales. Historical catches show that about 700 000 fin whales were caught in the Southern Hemisphere during the last century, more than from any other large whale population. However the Mori-Butterworth model suggests that there were originally only about 200 000 fin whales, far fewer than predicted by models without species interactions, because (according to the Mori-Butterworth model) fin whales benefited from extra krill made available through over-harvesting of blue whales.

The study addressed the second topic by investigating the interaction between species with slow and fast dynamics by using squid as an example of a species with fast dynamics. Interest in this arises because Mori and Butterworth (2006) concluded that fin whales were the first to benefit from the krill surplus followed by minke whales and crabeater seals, but in their model all species considered have relatively slow dynamics (see Chapter 2). Species with fast dynamics may instead have taken primary advantage of any krill surplus (see Chapter 5), which would change the predicted population trends of the other species.

What follows are first discussions of the models developed which were used to investigate the pre-exploitation abundance of fin whales together with the results obtained, and secondly discussion of the implication of the results obtained from the extended multispecies model of the system. Suggestions are also given for future research in order to improve the models.

6.1 Models developed to investigate pre-exploitation abundance of fin whales

Two simple models were developed: models GR_1 and GR_2 (Chapter 4). These models differ in the way that the growth rate of one species is affected by the presence of the other (see Figures 4.1 and 4.2). The study was undertaken for assessing whether these simple models can estimate lower pre-exploitation abundances of fin whales similar to that estimated by Mori and Butterworth (2006) (Chapter 4). The models include competitive interactions directly through a competition coefficient α. As the results show that there is not much difference between the values estimated by models GR_1 and GR_2 (Table 4.5), all trajectories plotted in Chapter 4 are based on model GR_2.

6.1.1 Species included in the models

Two species are included in the model: fin and blue whales. These predator species are competing for one prey, krill. Krill may move over large distances in the Southern Ocean. Fin and humpback whales inhabit all oceans, breeding in low latitude areas in winter and migrating to high latitude waters to feed in summer (Clapham *et al*., 1999). Although fin whales tend to occur in lower latitude areas than blue whales (Chapter 4) there is still likely to be competition between fin and blue whales because their distributions overlapped substantially historically. Blue whales were chosen as a competitor of fin whales in this model because of their history of intensive exploitation to near extinction, so that their impacts on the dynamics of fin whales, given a common food source in krill, are likely to have been substantial.

6.1.2 Areas investigated

The first area to be investigated by this study is Region A (Atlantic/Indian Ocean, IWC Management Areas II, III and IV see Figure 2.1). This is because the numbers of baleen whale harvested in the southern Atlantic/Indian Oceans were greater than in other regions off Antarctica (for example the southern Pacific Ocean) and hence likely caused greater impacts on the dynamics of these species.

The second area is Area III. As it is uncertain how large an overall fin whale population is represented amongst fin whales taken off Durban, these may relate only to this smaller region off Antarctica. Therefore the question posed is explored both for the case where this population extends to the full Region A, as well as if it relates to Area III only (see Chapter 4).

6.1.3 CPUE data from Durban

This study assumed CPUE to be proportional to whale abundance. The models compare data from Region A and Area III to CPUE data from whaling that took place off Durban. Fin whale CPUE was higher in the 1960's than in the 1920's, which suggests either lower abundance in the earlier period than in the later period, or fisheries targeted more on other species (such as blue whales) in 1920s than in 1960s. The model shows broadly similar trends to the CPUE indices for fin whales in the 1950s and 1960s both in Region A and Area III (Figures 4.7 and 4.9). However, the blue whale component does not show similar trends, with very low CPUE for the 1960s. In particular the models are unable to reflect the CPUE increase for fin whales from the 1920s to the 1960s, though this may mean that the CPUE data are not comparable over these periods. Nevertheless, further work to refine the model would be desirable.

6.1.4 Implication of the results – a closer look at fin whales

Results from this study corroborate the estimates obtained by the Mori-Butterworth Antarctic ecosystem model of an initial low number of fin whales. Knowledge of this pre-exploitation abundance of fin whales is essential to an assessment of the true impact of whaling on the Antarctic ecosystem, and to provide a good starting point for judging the past, current and future abundance of fin whales. This judgement has important implications for the management of any future whaling and for understanding the ecological role of fin whales (as explained below 6.1.4.1). The results could also selves as an important management of prey of this species. For instance in Figure 5.3 the model predicts that due to over-hunting of blue, humpback and fin whales an almost seven-fold of krill biomass increases.

6.1.4.1 How pre-exploitation abundance links with the future population

In general for marine resources, pre-exploitation abundance links with the future population as follows: if the pre-exploitation abundance of the population is over- or under-estimated, the level of recovery at any time will be correspondingly under- or over-estimated, and could lead to the resource being wasted or an increase in pressure to resume hunting of a depleted populations arising prematurely (Jackson *et al.*, 2008). It could also confound the interpretation of future responses of whale populations to environmental and other induced changes, such as global warming and overfishing by humans (Pauly, 1995; de la Mare 1997; Baker and Clapham, 2004). Ecological changes could alter the dynamic response of recovering whale populations, and could affect carrying capacity (Chapter 4). The carrying capacity of an environment may vary for different species and may change over time due to a variety of factors including food availability.

6.2 Extended Mori-Butterworth Antarctic ecosystem model

Chapter 5 extends the Mori-Butterworth Antarctic ecosystem model by adding one predator taken to be squid. Squid are a fast growing species and they have a short life span of not more than two years (Chapter 3). The impact of their fast dynamics for species such as whales and seals with slow dynamics was assessed (Chapter 5), and the model results suggest that fast growing species might have been the first to benefit from the krill surplus.

6.2.1 Implication of the results – adding a species with fast dynamics

Although the results obtained indicate that the inclusion of a species with fast dynamics has qualitatively little impact on the model outputs overall, squid were nevertheless possibly the first species (together perhaps with fast growing fish that are also krill predators) to benefit from a krill surplus (see Figure 5.3). This work is not meant to be exhaustive, but rather to stimulate dialog. To the author’s knowledge, this work is the first effort to synthesize such detailed information on squid to investigate their impact when interacting with species with slow dynamics. Some caution is warranted in interpreting these results, however. In all cases key parameters had to be inferred because they were not explicitly available or estimable. Thus this study has served a useful purpose as a guide for understanding the interplay between species with slow and fast dynamics. It could also serve as a prototype for future planning, implementation, and management of fisheries for fast dynamics species in the Southern Ocean.

6.3 Key findings

The present study summarizes the key findings in Chapter 4 and Chapter 5. Among the matters that the study addresses is to summarize data (used in Chapters 4 and 5) and information available. One of the findings in Chapter 4 is that the gaps in data (CPUE data whaling off Durban) availability are apparent. A general shortcoming in Chapter 4 is the lack of data collection between 1900 to 1919 and 1928 to 1953. The following are the general findings in Chapter 4 and Chapter 5.

6.3.1 Improve understanding on abundance of fin and blue whales for Area III

Chapter 4 estimates the pre-exploitation abundance of fin whales by investigating Region A and Area III. The purpose was to assess how this pre-exploitation abundance of fin whales relates to that estimated by Mori and Butterworth (2006), and good agreement was found. Furthermore the study intended to check if Region A and Area III represent the same stock by comparing their results with CPUE data from the whaling that took place off Durban. Although further work is needed, the results are similar whether one looks at Region A or Area III only.

6.3.2 Which species benefited first from krill surplus

Krill abundance in the Southern Hemisphere likely increased after the reduction, to near extinction, of large baleen whales (Branch *et al.*, 2004; Sirovic *et al.*, 2004; Mori and Butterworth, 2006). This study investigated the interactions between species with fast dynamics (such as squid) and slow dynamics (such as whales and seals). The results suggest that species with fast growth were the first to benefit from a krill surplus, before minke whales and crabeater seals as suggested by the Mori-Butterworth Antarctic model (Figure 5.2).

6.3.3 Sensitivity to parameter values assumed for squid

Among the scenarios examined in the sensitivity tests were the initial abundance of squid and the parameter η governing the density dependence of natural mortality and/or birth rate of squid. The study found that η was one of the parameters to which results were most sensitive, and hence explored sensitivity to this parameter (see Chapter 5). The model results suggest however that the squid biomass trajectories are relatively insensitive to the initial squid abundance assumed (Figures 5.2 (c) and (b) respectively).

6.3.4 Squid links to environmental change

In Chapter 3 it is argued that squid have very fast growth rates, short life spans and therefore rapid population turnover. Due to this, squid dynamics link to environmental variability and the response of squid may be complex (Miyahara *et al.,* 2006; Pecl and Moltschaniwsky, 2006; Markaida, 2006; Vidal *et al.*, 2006; Xinjuni *et al.*, 2007). Understanding these links could have the potential to dramatically alter population model predictions. However it is difficult to suggest with any certainty what the impacts of environmental change will be on the squid population or its biology.

6.3.5 The need for squid data

As there were no data available for squid for use in fitting the model, all squid parameters were fixed (Chapter 5). Although there are some catch data for squid (for example annual catch between 1985 to 1996 as listed in Gonzalez *et al.,* 1997), no suitable data series were available for this study. Fishery independent data are also desirable to compare with model predictions before the implications of this work for management of the squid fishery might be considered.

6.4 Future work

Future research could include the following:

a) It would be desirable to fit the model to available squid abundance or/and trend data, and perhaps to extend the model to an age- disaggregated form. However moving from an age-aggregated to age-disaggregated approach has some difficulties, for example increased data requirements and complexity of the model (see Chapter 1). Comparison with other age-disaggregated models such as MULTSPEC, GADGET or MSM (see Chapter 1) would also be useful to see whether results from these models are similar.

b) As appropriate, future research should include a fuller understanding of predator prey relationships, especially about which species of whales and seals to include in the model as predators of squid (Croxall, 1992). It would be interesting to compare the results of these models with studies which investigate the effect of environmental changes on the system (for example Wiedenmann *et al*., 2008), which could have substantial impacts on whale and seal populations.

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